REVISIONS OF *AGENIUM* AND *HOMOZEUGOS* (POACEAE): INTEGRATING CLADISTIC ANALYSIS AND GEOGRAPHIC INFORMATION SYSTEMS

By

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This work is dedicated to my parents:

Gerald and Lois Guala

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by

Gerald F. Guala II

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Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

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By

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Chairperson: Walter S. Judd
Major Department: Botany

Revisions of the genera *Agenium* and *Homozeugos* are presented. A cladistic analysis of ITSI&II nuclear ribosomal DNA sequences confirms that they form a monophyletic group with *Trachypogon* (Poaceae: Andropogoneae). Morphology-based cladistic analyses were conducted for both *Agenium* and *Homozeugos*. Three species are recognized within *Agenium*. The two smaller but more widely distributed species, *A. leptocladum* and *A. villosum*, form a clade sister to *A. majus*. Six species of *Homozeugos* are recognized. These include one newly described species, *H. conciliatus*. Within *Homozeugos*, *H. fragile* and *H. katakton* form a clade that is sister to the remaining four

species of the genus. Within the other clade, *H. eylesii* sister to the rest, with *H. conciliatus* sister to *H. huillense* and *H. gossweilerii*. A geographic information system was compiled using 45 layers of spatial environmental data. Soil chemical, physical, and color analyses were also done on samples from every collection made for this study. These data were integrated with the distributions of the species to predict their possible distributions. The spatial data were then integrated with the cladograms generated here and resulted in the determination that several monthly mean values for precipitation and hours of sunshine as well as temperature and dry season vegetation are correlated with cladogenesis in *Homozeugos*.

CHAPTER 1
INTRODUCTION

This study examines some of the factors that are correlated with cladogenesis, and hence biodiversity, in two genera of tropical savanna grasses and provides the groundwork for much more detailed examinations in the future. For many years, investigators have attempted to determine the factors that produce biodiversity as well as those that determine its spatial extent. These investigations have generally examined the relationship between areas or habitats and the number of species occurring within them. Those with the highest number of species were deemed most conducive to the maintenance or production of biodiversity, depending on the philosophical leanings of the investigator. These studies have often suffered from inexplicit and outdated taxonomy as well as a horizontal structure that examines only a slice (usually at the species level) through the phylogenetic tree that encompasses biodiversity. In this study I have taken a different route by first generating explicit, well supported phylogenetic hypotheses and then examining the correlation

of specific spatially varying habitat characteristics with all of the possible clades within those phylogenetic hypotheses. Rather than yielding a group of areas where biodiversity resides, this method has the potential to yield a group of spatial characteristics that are correlated with the factors that play a role in the actual production of biodiversity.

Environmental history clearly plays a role in the diversification of clades. A very useful method of applying environmental data to cladograms, "historical ecology" (Brooks and Mclennan 1991, 1993), requires a well supported historical model of the area or process being examined. However, it is not necessary to know the exact sequence of a large set of combined environmental events that have occurred in a specific geographic area, in order to be able to relate the environment to phylogenetic history. This is true because in the absence of a good fossil record, there is no reason to assume that a given taxon evolved and diversified in a given geographic place just because it happens to reside there now. A more realistic model is that of evolution within a given "niche" that may or may not have been spatially stationary in history. This is the model of "habitat plates" advanced by Vrba (1993) as part of her "habitat theory" (Vrba 1992) and it is the reason that I am

not making a historical biogeographic argument here. I advance only a historical argument that can be overlain onto paleogeography to test the hypotheses that result from it.

The investigations of two large areas of different continents with very different post-Cretaceous climatic histories (Coetzee 1993, Romero 1993) allow the study of the interaction of enormously different scales of mobility and change in environmental parameters (e.g., migration of precipitation isoclines vs. relatively horizontally stationary elevational change). I seek to compare the spatial variables correlated with speciation in two related genera of grasses growing in similar habitats on different continents. Of all of the app. 600 genera of grasses, only *Agenium* Nees and *Homozeugos* Stapf are closely related, grow in similar habitats on South America and Africa respectively, and have enough species to have a sufficient number of internal nodes in their cladograms but not so many species as to be unmanageable. They are also wind pollinated and widely distributed within the savanna habitats on their respective continents, thus insuring a large sample of the spatial environment on each continent without the confounding effects of pollinator ranges and behaviors. They form a well supported clade, along with *Trachypogon* Nees, which is widely distributed in Africa,

Central America, and South America (Kellogg and Watson 1993, and this study).

Cladistic analysis has brought about a revolution in systematics by allowing the generation of explicit and testable phylogenetic hypotheses required for this type of study. The phylogenetic hypotheses in this investigation were derived from cladistic analyses using morphology and anatomy within the genera, with the addition of DNA sequences to independently test Kellog and Watson's (1993) hypothesis of generic relationships, which had been derived from morphology and anatomy. The Phylogenetic Species Concept, PSC (Donoghue 1985, Mishler 1985, Mishler & Brandon 1987) provided the explicit and robust delimitation of species required in this study.

Geographic Information Systems (GIS's) have brought about a revolution in the spatial analysis of data by combining the analytical power of relational database structure with highly accurate georeferenced spatial displays. A very large number of existing data sets of worldwide coverage have been incorporated into Geographic Information Systems and have been made readily available on common desktop computer systems (e.g. NOAA-EPA Global Ecosystems Database Project 1992, National Climatic Data Center 1992, 1994). However, the explosive growth in

computing power and information dissemination over the course of this study has been a great asset while at the same time making the technology and the resolution of the data used obsolete. A simple query on AltaVista revealed that the number of sites including the phrase "Geographic Information Systems" on the world wide web (WWW) at the beginning of this study (August 1992) was four, and the number of sites including the phrase as of 20 February 1998 was 28,258. On a more personal note, I began this study with the the standard desktop system at the time. During the course of this study I have translated my data through eight versions of three different GIS software packages, installed 24 times the amount of RAM and 26 times the amount of disk space that was originally present in my computer, and the system still does not meet the University of Florida's requirement for the basic minimum system (for incoming freshmen in the Fall of 1998). Clearly, the GIS presented here should be thought of as a simple starting paradigm for future, higher resolution systems rather than as a static data set for future analyses.

Even with such a small system, I have been able to build a globally comprehensive integrated system of 45 environmental variables to both predict where the species of *Agenium* and *Homozeugos* can live and to identify a few

tantalizing spatial environmental variables that are correlated with cladogenesis. These accomplishments are in addition to the production of the two complete monographs presented here, which include phylogenetic analyses, keys, nomenclature and descriptions, as well as the most comprehensive habitat descriptions available.

CHAPTER 2
A REVISION OF *AGENIUM*

Introduction

The genus *Agenium* is a member of the Andropogoneae (Poaceae), occurring on the cerrados of South America from Uruguay and central Argentina north over much of Brazil, Paraguay and Bolivia. Members of the genus provide forage for both native and domestic animals and help to stabilize fragile cerrado soils.

First described by Nees (1829) as *Heteropogon villosus* and then as *Agenium nutans* (Nees 1836), *Agenium villosum* (Nees) Pilger was the first species in the genus to be recognized. Nees (1836) recognized the genus on the basis of the homogamous spikelet pairs present at the base of the racemes. All three species of *Agenium* are quite variable in phenotype and there have been several species and infraspecific taxa published to account for this variability. This has resulted in great confusion over the years. To rectify the situation the genus is here revised and the taxonomy is updated to reflect the explicit hypothesis of phylogeny generated in this study.

Materials and Methods

Molecular Studies

All material of *Agenium,* as well as the related genera *Homozeugos* and *Trachypogon*, used for molecular work is vouchered at FLAS. Standard C-TAB extractions were performed according to the method of Doyle and Doyle (1987). These were made from air dried specimens of *Agenium, Homozeugos*, and *Trachypogon* collected by the author. Those that ultimately yielded usable sequences are Guala 1617, 1621, 1643, 1648 and 1765. Sequences of species of all other genera were generated by Johan Spies, and obtained from E.A. Kellogg (pers. com.). All have been deposited in Genbank. The ITS I & II regions and the included 5.8S gene were amplified by PCR in 75 µl reactions using the primers (4&5) described by Baldwin (1992) employing 35 cycles and an annealing temperature of 51°. *Homozeugos eylesii* was amplified using the Baldwin 5 primer and the internal ITS-2 primer to amplify only the ITS-I region because it failed to amplify under the protocol described above. Amplified fragments were then purified using Promega Wizard™ minicolumns and cycle sequenced using ABI dye terminator mix, and 25 cycles.

DNA samples were then dried down and sequenced at the Iowa State University Sequencing Facility. The returned data files were assembled and edited as described by Pridgeon et al. (1997).

Morphology and Anatomy

Herbarium specimens representing the known range of variation in *Agenium* were made by the author from natural populations throughout its geographic range (see Figures 2-6, 2-8 & 2-10). A total of 328 sheets representing all known populations of *Agenium* were borrowed from AA, BAA, BM, BR, CTES, GH, MO, NY, SI, TAES, UC and US. Specimens at IBGE, PRE, R, RB and UB were measured at those herbaria. All available specimens were scored for the macro-morphological characters included in the descriptions below. At least five replicates of most measurements were made per collection (when possible). Height was measured in the field from my own collections and was taken from randomly selected individuals within the population. Transverse sections of leaves of all of my own collections were prepared and observed as described in Guala (1995). Leaf specimens from the midpart of mature midculm leaves of all of my collections also were prepared as described by Guala (1995) for observation under the SEM. All samples were

digitally photographed at 90X across their entire surface and then several representative photos from each side were taken at higher magnifications. These were saved as 1024 X 768 Tiff files and databased with the other morphological data.

Both the morphological and molecular data sets were analyzed using parsimony with PAUP 3.11. In the molecular data set, the general heuristic algorithm was employed using 100 random replicates. The results were confirmed using PAUP* 4.0 with the branch and bound algorithm. In the morphological analyses, the branch and bound algorithm was used.

The original OTU's were 21 separate entities corresponding to populations or putative meta-populations that appeared to be clearly internally consistent and homogeneous. Upon measurement of all characters it became clear that these entities fell into only three diagnosable groups. There was overlap in the distribution of every character state within each of the groups and no individual or group of individuals within a group could be explicitly described (or diagnosed) as a different entity. These three were the groups used as OTU's in the cladistic analysis of the ingroup. The phylogenetic species concept (PSC) of Donoghue (1985), Mishler (1985), and Mishler and Brandon

(1987) was employed in this study. The study is based on the assumption that diagnosable evolution (cladogenesis) occurs at low taxonomic levels making species diagnosable phylogenetic units in an evolutionary hierarchy. This "history based" (Baum and Donoghue 1995) definition of species, therefore, is considered appropriate. The theoretical pitfalls of applying the concept of monophyly at the species level are well publicized and an alternative PSC has been proposed to circumvent the problem (Nixon and Wheeler 1990, 1992, Davis and Nixon 1992, Davis 1993). This alternative PSC can be called "character based" because it relies only on the distribution of unpolarized characters, thus negating inference of prior evolution. Because I used only characters with states that are discrete between OTUs and ubiquitous within them and because I only (operationally) lumped together local populations for which I could find no diagnosable differences, the grouping requirements for the alternative PSC are met for the designation of OTUs (not species) in this study. However, as a ranking criterion for the species level, I believe thatthe original PSC (Donoghue 1985, Mishler 1985, Mishler & Brandon 1987) is much more informative and philosophically appealing for this type of study.

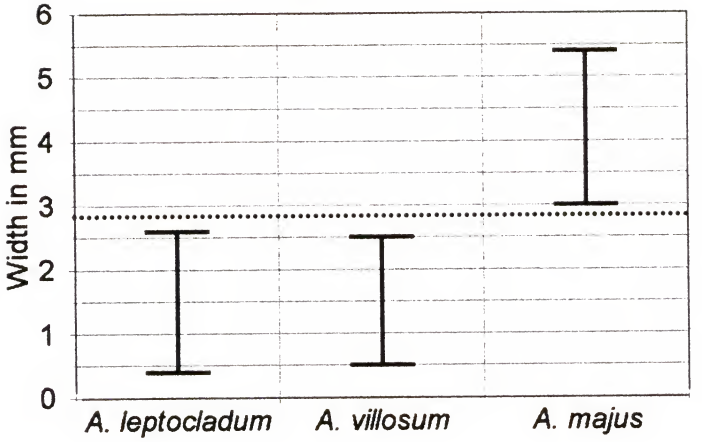
A large number of characters including length of all major parts and appendages were originally measured. Degree and type of pubescence as well as surface texture and shape were also measured. The characters in Table 2-1 are those that showed informative distributions among the OTUs and were subsequently used in the cladistic analyses. Most of these characters are self explanatory, with the exception of character 10. There are, in fact, two types of macrohairs on the surface of the first glume of the pedicellate male spikelets in *Agenium villosum*. All three species often have appressed, long, stout hairs that occur near the tip of the glume and sometimes along its upper edges. In *Agenium leptocladum* there are usually one to five of these hairs at the tip of the glumes, especially those near the distal tip of the inflorescence. All three species also have hermaphrodite sessile flowers that are villous, due to spreading hairs that commonly have inflated bases. *Agenium villosum* has these spreading hairs on the pedicellate spikelets as well and with the exception of a single population of *A. leptocladum*, the other two species do not (this population of *A. leptocladum* is discussed below).

Table 2-1. Table of morphological characters used in the cladistic analyses of *Agenium*.

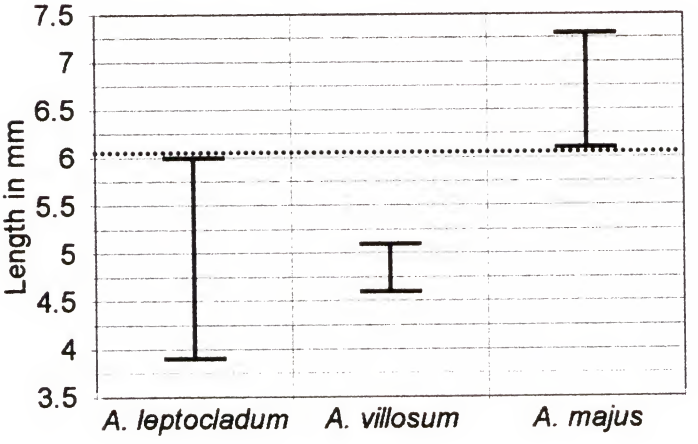
	State 0	State 1
1	Panicle with a single racemose segment.	Panicle with 2-many racemose segments.
2	Midvein of leaf lamina small and inconspicuously green.	Midvein of leaf lamina large and conspicuously yellow to white.
3	Nodes of the basal half of the culm > 2.7 mm in diameter.	Nodes of the basal half of the culm < 2.7 mm in diameter.
4	Plants with 5 or more basal leaves with blades longer than those of the midculm leaves.	Plants no basal leaves with blades longer than those of the midculm leaves.
5	The leaf lamina with fiber strand(s) directly interior to the bulliform cell strands.	The leaf lamina without fiber strand(s) directly interior to the bulliform cell strands.
6	First glume of the basal spikelet > 6.1 mm long.	First glume of the basal spikelet < 6.1 mm long.
7	Palea of staminate spikelet > 3.5 mm.	Palea of staminate spikelet > 3.5 mm.
8	Leaf lamina abaxial surface with papillae	Leaf lamina abaxial surface without papillae
9	Basal cell of the bicellular microhairs longer than the distal cell.	Basal cell of the bicellular microhairs shorter than the distal cell.
10	Pedicellate spikelets villous.	Pedicellate spikelets not villous.
11	Basal leaves > 1/3 of the plant height.	Basal leaves < 1/3 of the plant height.
12	Papillae of the abaxial leaf laminar surface longer than wide.	Papillae of the abaxial leaf laminar surface not longer than wide.

Figure 2-1. Ranges of characters 3, 6 and 7.

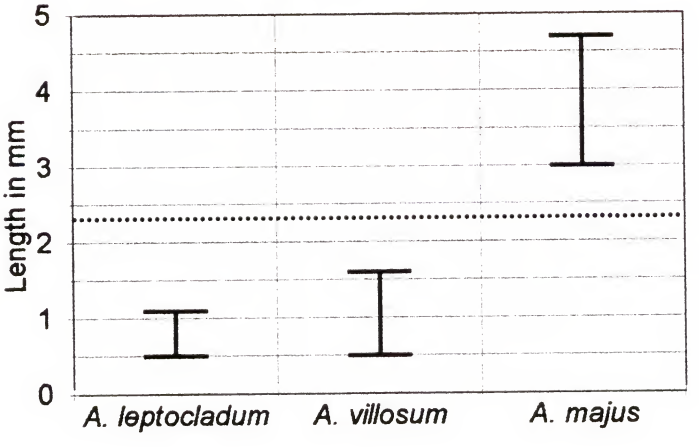
3. Width of Nodes
Agenium



6. First Glume Length
Agenium



7. Length of Fertile Palea
Agenium



All measured characters used here are delimited on the basis of a gap in the otherwise continuous variation within the clade.

Phylogenetic Analysis

In the cladogram of Kellogg and Watson (1993) *Agenium* is a part of a clade with *Trachypogon* and *Homozeugos.* In their cladogram it is supported by five synapomorphies: ligule an unfringed membrane, spikelets all in heterogamous combinations, callus long, callus pointed, lower glume not two-keeled (reverses in Trachypogon) (E. Kellogg pers. comm.). For this study, an analysis of sequences from the internal transcribed spacer region (ITS) of the nuclear ribosomal DNA of several genera of the Andropogoneae was performed to test the monophyly of this clade, its component genera, and to determine outgroup relationships for use in the cladistic analysis of *Agenium*. This study confirmed the monophyly of the *Agenium+Homozeugos+Trachypogon* clade as well as the sistergroup relationship of *Agenium* to the *Homozeugos+Trachypogon* clade (Fig. 2-2). The *Homozeugos+Trachypogon+Agenium* clade is defined by at least eight synapomorphies in both of the trees (Fig. 2-2).

Figure 2-2. Cladogram based on ITS sequences of several species in genera of the Andropogoneae. Two topologies were found. They differ only in the placement of *Heteropogon contortus,* as shown. The unshown portion of the alternative tree is identical to the one shown. Both trees have a length of 428 steps, CI = 0.708, HI = 0.292, RI = 0.573, and RC = 0.406; trees were generated from a heuristic search of 100 random addition replicates; (TBR) tree-bisection-reconnection-branch-swapping was used in PAUP 3.3, and confirmed with a branch and bound search in PAUP*. Bootstrap support (using the same parameters as above) for the *Trachypogon+Homozeugos+Agenium* clade is 73%.

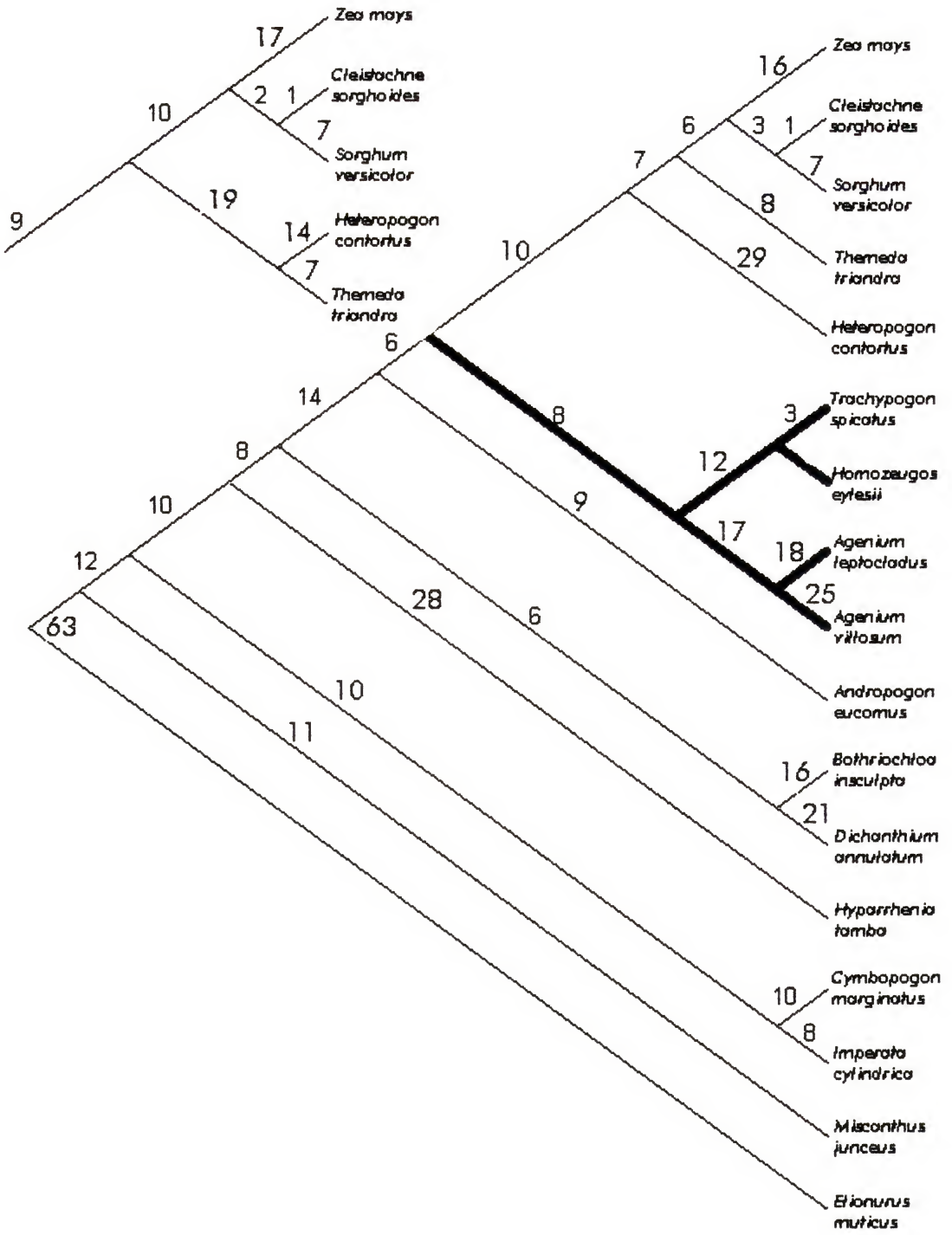
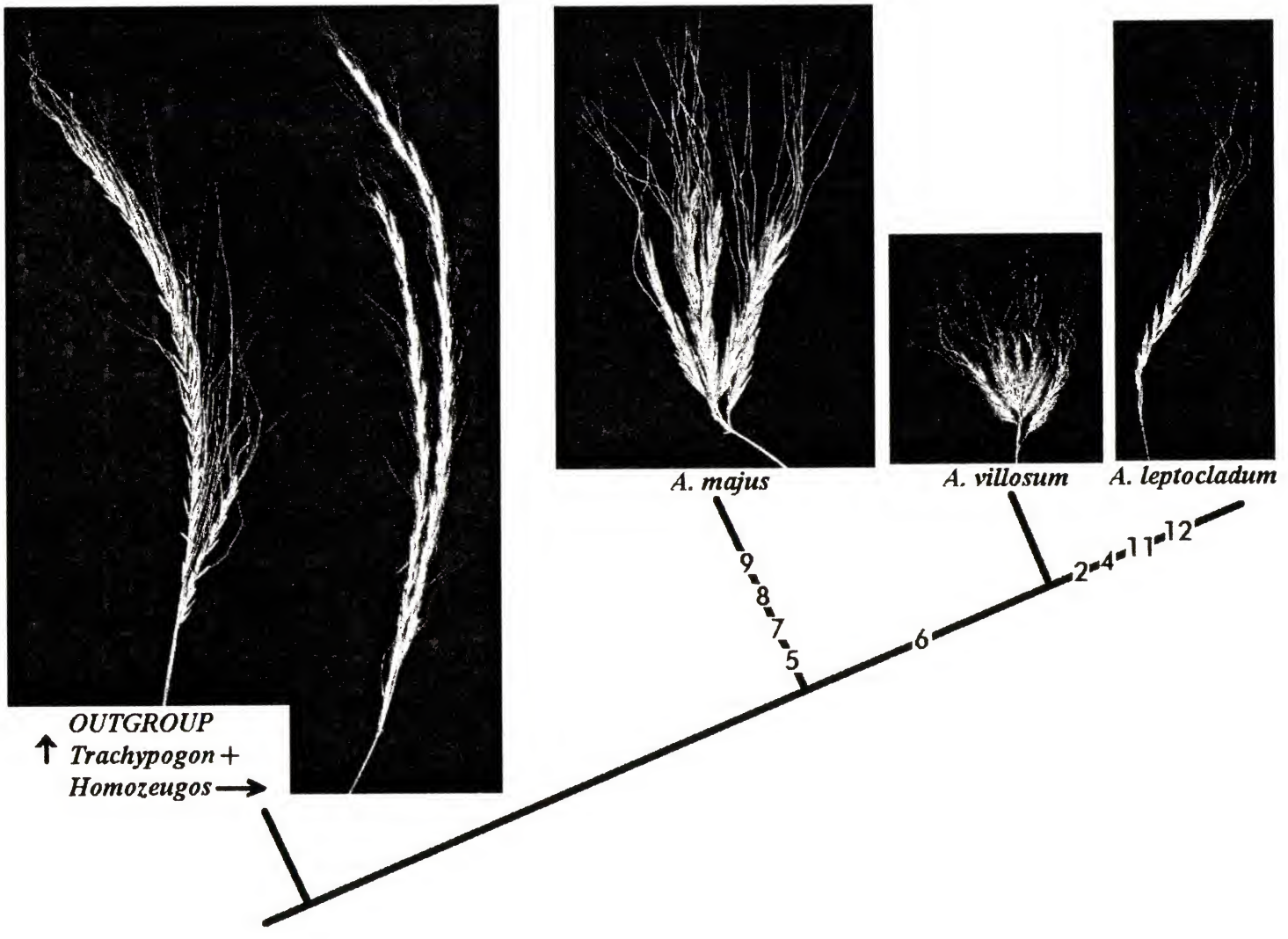

Zea mays
Cleistochne sorghoides
Sorghum versicolor
Heteropogon contortus
Themeda triandra
Trachypogon spicatus
Homozeugos eytesii
Agenium leptocladus
Agenium villosum
Andropogon eucomus
Bothriochloa insculpta
Dichanthium annulatum
Hyparrhenia tamba
Cymbopogon marginatus
Imperata cylindrica
Miscanthus junceus
Elionurus muticus

Table 2-2. Table of character state distributions for the species of *Agenium* and the outgroup: *Trachypogon+Homozeugos.* Variable character states are designated by "9".

	1	2	3	4	5	6	7	8	9	10	11	12
A. leptocladum	0	0	1	1	1	1	1	0	1	9	1	0
A. majus	1	1	0	0	0	0	0	1	0	1	0	1
A. villosum	1	1	1	0	1	1	1	0	1	0	0	1
Trachypogon	9	1	9	0	9	0	1	0	1	9	0	1
Homozeugos	9	1	9	0	1	0	9	0	9	0	0	1

Figure 2-3. Cladogram of relationships within *Agenium*. Tree Statistics: 12 characters, 12 steps, CI = 1.0, RI = 1.0, RC = 1. Numbers refer to character numbers in Tables 2-1 and 2-2.


A. majus
A. villosum
A. leptocladum
OUTGROUP
Trachypogon +
Homozeugos
9
8
7
5
6
2
4
11
12

The monophyly of *Agenium* and the *Homozeugos+Trachypogon* clade are strongly supported.

The ingroup analysis of *Agenium* was conducted using 12 morphological characters (see Tables 2-1 and 2-2). It resulted in a single most parsimonious cladogram (Fig. 2-3). In this cladogram, A. majus is sister to a clade comprised of *A. villosum* and *A. leptocladum*. The *A. villosum* + *A. leptocladum* clade is united by the presence of a short first glume in the basal hermaphrodite spikelet.

Discussion

The monophyly of the *Trachypogon+Homozeugos+Agenium* clade and the sister group relationship of *Trachypogon+Homozeugos* to *Agenium* as well as the monophyly of *Agenium* are supported by both morphology (Kellogg and Watson 1993) and ITS sequences. Although Kellogg and Watson (1993) did not list what the character states were that supported the monophyly of *Agenium*, they did have five characters supporting it. The sessile hermaphrodite spikelets are so similar among the species of *Agenium* that they are almost indistinguishable. The homogamous spikelets at the base of the raceme are a good synapomorphy, occurring only very rarely and sporadically outside of this genus.

The only other character that I can find that is clearly an autapomorphy for the genus is the peculiarly grooved lower glume of the sessile hermaphrodite spikelet. A few other genera exhibit a lower glume that can be described as having a groove but in these the groove does not resemble that of *Agenium*. It is clear that these genera are not closely related to *Agenium*. There may be other synapomorphies for the genus (as evidenced by Kellogg and Watson 1993) but the Andropogoneae are such a diverse and homoplasious group that I doubt whether there are other non-homoplasious morphological characters that support its monophyly. Traditionally, *Agenium* has been included in *Heteropogon* (Roberty 1960, Parodi 1962, Hackel 1885) presumably due to the striking resemblance (in general form) of *A. leptocladum* to immature specimens of *Heteropogon contortus*. It was only with Clayton's (1972) recognition of the striking similarity between the flowers of *Agenium* and his subsequent support of the genus that it gained wide acceptance. The present study clearly supports the recognition of *Agenium* as a genus based on both molecular and morphological characters.

The sister group relationship of *Agenium majus* to the *A. leptocladum* + *A. villosum* clade is supported as well. This conclusion is in conflict with the views of Roberty (1960) that *A. villosum* is the closest relative of *A. majus*.

Roberty's assesment was based on the resemblance of *A. villosum* to *A. majus* in general form in the inflorescence and overall habit. This study has shown that the characters that produce the resemblance of these two species are symplesiomorphic and hence, not useful for recognition of taxonomic groups. The support for the *A. leptocladum + A. villosum* clade hinges on the character of short hermaphrodite spikelets (represented by the length of the first glume). It is not appropriate to employ decay analysis on such a small data set, however, it is instructive to note that given different outgroup states, the data set has 6 characters that could potentially support the *A. leptocladum + A. villosum* clade; the one actually supporting it now and the five synapomorphies for *A. majus*, and only 5 that could potentially conflict with it and support a grouping of *A. majus and A. villosum.* Only character 10 (pedicellate spikelets villous or not) would support an *A. majus + A. villosum* clade and as I have pointed out, this character is somewhat variable. Five of the characters could be polarized in either direction by use of a single species within the outgroup clade rather than the entire clade as an outgroup. Although both *Homozeugos gossweilerii* Stapf and *Trachypogon macroglossus* Trin. provide polarizations that lead to homoplasy in the tree, no

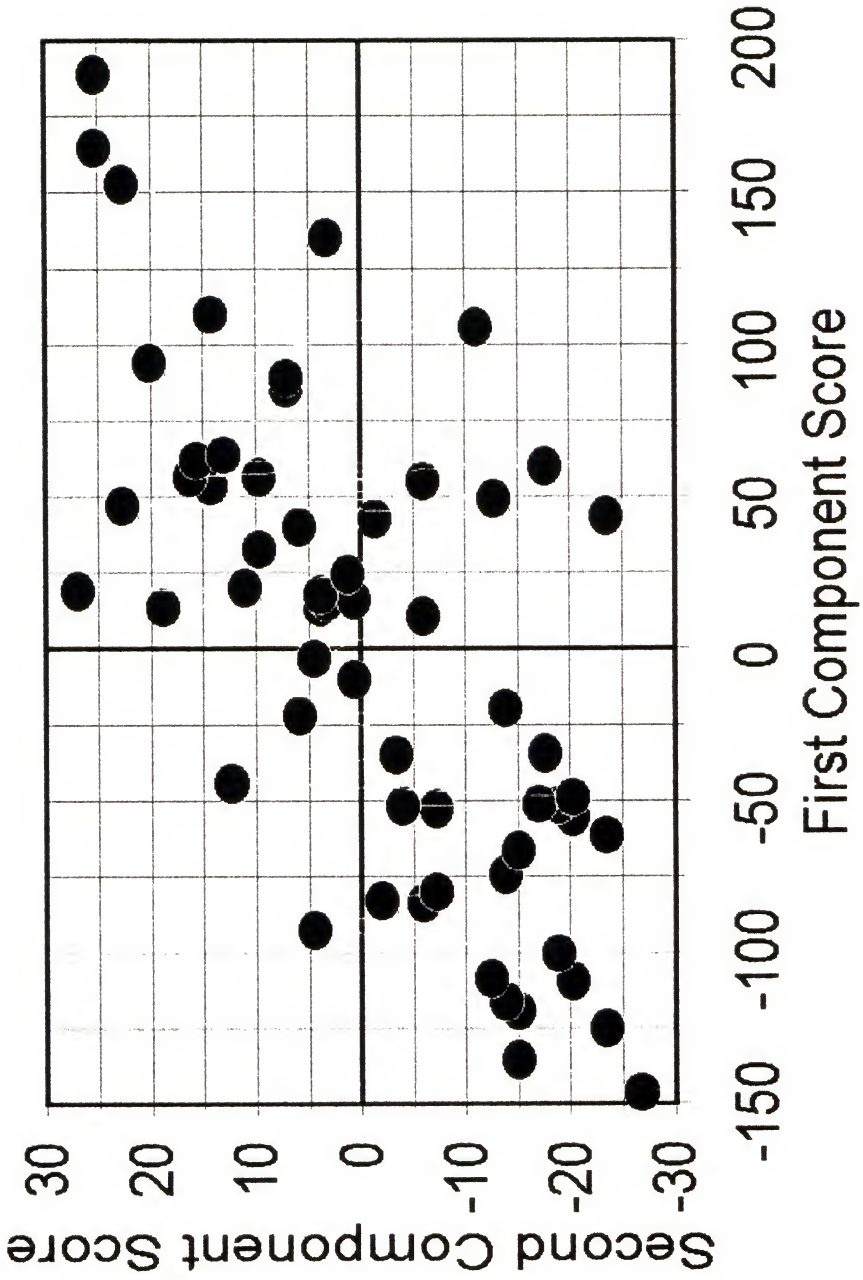
species in the outgroup provides a polarization of character states that will produce an equivocal or conflicting topology in the consensus tree.

The results of this analysis are also relevant to the question of species limits. Given that species are here considered to be the minimum diagnosable monophyletic units (Donoghue 1985, Mishler 1985, Mishler & Brandon 1987), it seems wholly inappropriate to formally recognize subspecific taxa, which would lead to the recognition of paraphyletic groups. All of the characters used to diagnose the subspecific taxa previously described in this genus (e.g vestiture, plant robustness and size) have been measured and found to vary across subspecific and often specific boundaries. The only major species level readjustment required by this study is the inclusion of *Agenium goyazense* within *A. leptocladum*. Hackel (1901) diagnosed *Andropogon goyazensis* (= *Agenium goyazense*) as a more robust, less branched form, with a "different" vestiture. All of these supposedly diagnostic characters often vary greatly within single populations, especially in the northern part of the range of *A. leptocladum*. I have found no characters that reliably separate *A. goyazense* from *A. leptocladum*.

Table 2-3. List of Characters used in the Principle Component Analysis of *Agenium leptocladum*.

Character Name	**Description**
LIGAVG	Mean ligule length.
LIGMAX	Length of the longest mature ligule.
LIGMIN	Length of the shortest mature ligule.
LLAVG	Mean leaf length.
LLMAX	Length of the longest mature leaf blade.
LLMIN	Length of the shortest mature leaf blade.
LWAVG	Mean leaf width.
LWMAX	Width of the widest leaf.
LWMIN	Width of the thinnest leaf.
NODEAVG	Mean node width.
NODEMAX	Width of the widest node.
NODEMIN	Width of the thinnest node.
SPIKEAVG	Mean spikelet length.

Figure 2-4. Principal Component Analysis of 59 populations of *Agenium leptocladum s.l.* using 12 vegetative characters and raceme length. The first two components are plotted. The percent of total variation described by the first component is 63.52 and the percent of variation described by the second component is 21.01.


Second Component Score
30
20
10
0
-10
-20
-30
-150
-100
-50
0
50
100
150
200
First Component Score

In fact, a majority of collections match the descriptions of both species equally well. This has been confirmed by Filgueiras (in prep.).

Agenium leptocladum is a widespread and variable species and shows a great diversity in habit and size. A Principle Components Analysis was run using 12 characters and all collections of *Agenium leptocladum* (see Fig. 10 and Table 3). No discernable phenetic groups were observed within the species. The monophyletic species, *Agenium leptocladum*, as recognized here, is well delimited by its general habit as well as the copious and longer-than-wide papillae of the abaxial leaf surface.

Although once locally common, *Agenium majus*, has not been collected in more than 30 years and, despite an intensive effort, could not be relocated. It may be extinct. The four original collection localities specific enough to be located are all dominated by *Brachiaria decumbens*, an introduced African forage grass. The other two species have at least two populations each in protected areas and are still found in many localities in natural pasture but have clearly undergone considerable loss of diversity due to pasture conversion and development. They will no doubt continue to decline as the destructive exploitation of the cerrado continues.

Taxonomic Treatment

Agenium Nees in Lindley, A Natural System of Botany. 447. 1836. TYPE SPECIES: *Agenium nutans* Nees

Strongly to weakly caespitose perennials. Rhizomes short, to ca. 1 cm long. Bud scales white-wooly to glabrate, often becoming stramineous. Culms erect to decumbent, not rooting at the nodes, to 203 cm tall (as measured from the base of the culm to the base of the inflorescence), the nodes puberulent to villous, becoming glabrous with age. Leaves green to weakly glaucous, with their blades longer than the sheaths, flat, glabrous to pilose; blade 2.5-78 cm long, 0.9-10.2 mm wide, minutely antorsely scabrous on the margins, showing the characteristic C_4 (XyMS type) anatomy in cross section; ligule a hyaline membrane, variable in shape, its margin white translucent to opaque burnt umber, often minutely fringed. Inflorescence a panicle with 1-24 racemose segments, the spikelets in the basal portion of each segment homogamous staminate. Sessile staminate spikelets unawned, with an obliquely attached callus; first glume 6.0-15.1 mm long, its lamina generally asymmetrical with two minutely

scabrous to long pilose keels appearing as the margins, the marginal lamina strongly appressed to the adaxial surface of the lamina, the abaxial surface glabrous to minutely papillate to villous; second glume completely or nearly symmetrical, less indurate than the first glume; sterile lemma hyaline; fertile lemma hyaline in the lower part and edges, indurate elsewhere; palea to ca. 4.7 mm; stamens 3; lodicules cuneate. Pedicellate staminate spikelets generally resembling the sessile staminate spikelets. Sessile hermaphrodite spikelets, with a callus 0.3-2.7 mm long, obliquely attached; first glume 3.9-7.3 mm long, the lamina generally symmetrical, indurate, with a distinct longitudinal groove, strigose to villous; second glume symmetrical, indurate, with a distinct longitudinal ridge; sterile lemma hyaline, awned, the awn antorsely scabrous, generally twisted and geniculate; fertile lemma hyaline; palea to 4.0 mm long; lodicules cuneate. Diaspore composed of the entire hermaphrodite spikelet with its callus. With the awn and its attached lemma deciduous upon dispersal. The fruit a caryopsis with a longitudinal groove.

1. Inflorescence with a single raceme; leaves primarily cauline, their midveins inconspicuous.1. *A. leptocladum*

1. Inflorescence with 2-10 digitate to subdigitate racemes;

leaves primarily basally disposed, their midveins prominent and lighter than the lamina. 2

2. Culm nodes > 2.7 mm wide on the basal half of the culm; first glume of hermaphrodite fertile floret > 6.1 mm long; palea > 3.5 mm long. . . . . 2. *A. majus*

2. Culm nodes < 2.7 mm wide on the basal half of the culm; first glume of hermaphrodite fertile floret < 6.1 mm long; palea < 3.5 mm long. . . . . 3. *A. villosum*

1. *Agenium leptocladum* (Hackel) Clayton, Kew Bulletin 27: 447. 1972.

Andropogon leptocladus Hackel, Flora 68: 122. 1885. *Sorghum leptocladum* (Hackel) Kuntze, Revision Generum Plantarum 2: 792. 1891. *Heteropogon leptocladus* (Hackel) Roberty, Boissera 9: 144. 1960. TYPE: Paraguay, in pascuis, 1875. Balansa 222 (=222a)(holotype, W!, US Accession #00156676 fragment from W!; isotypes, K, W!).

Andropogon leptocladus Hackel f. *simplex* Hackel, Extrait du Bulletin de l'Herbier Boissier. 2nd ser. 4: 268. 1904. TYPE: Paraguay, in arenosis Cordillera de Altos, Hassler 3766 (not seen).

Heteropogon leptocladus (Hackel) Roberty var. *pilosus* Parodi, Revista Argentina de Agronomia 28: 120. fig. 4. 1962. TYPE: Argentina, Prov. Corrientes, Dep. Concepcion, Rincon de luna, sandy grasslands. 26 Feb. 1961. T.M. Peterson 5807 (holoytpe: BAA!).

Andropogon goyazensis Hackel, Oesterreichische Botanische Zeitschrift 1901. 51: 152. *Agenium goyazense* (Hackel) Clayton, Kew Bulletin 27: 447. 1972. TYPE: Brazil, Goiás, Glaziou 22571 (holotype: W!, isotype: K!).

Caespitose (sometimes weakly so) perennial. Rhizomes generally short but the culms often decumbent and running for several centimeters under the surface and rooting at the nodes in sandy soils. Bud scales often white wooly, becoming stramineous. Culms green to yellow, usually branching on the lower half, generally minutely puberulent at least distally, very rarely completely glabrous, 20-158 cm, the nodes 0.4-2.6 mm wide, puberulent to villous, becoming glabrous with age. Leaves glabrous to sparsely hirsute or pilose; lamina 2.5-24 cm long, 0.9-10.2 mm wide, linear to narrowly triangular, without a prominent midvein; margin minutely antorsely scabrous; ligule 0.1-6.1 mm long, truncate to dome-shaped, often with a prominent central lobe

and two smaller lateral lobes, minutely fringed to erose or entire. Inflorescence a single racemose panicle, 2.5-11 cm long with 6-24 spikelet pairs; spikelets in the basal portion homogamous; rachis segments between the basal homogamous spikelet pairs to 9 mm, those between the fertile pairs 0.5-4.2 mm. Sessile staminate spikelets with a callus 0.2-1.5 mm long, obliquely attached; first glume 6.0-11.6 mm long, the abaxial surface of the lamina glabrous to minutely papillate or villous; second glume 5.4-11.4 mm long, glabrous to villous, especially on the basal half and margins; sterile lemma 5.0-8.6 mm long; fertile lemma 4.0-8.6 mm long; palea inconspicuous, ca. 0.1 - 0.6 mm long; anthers 2.3-5.9 mm long; lodicules ca. 0.6 mm long. Pedicellate staminate spikelets on a pedicel 0.5-3.5 mm long, with the callus 0.4-1.8 mm long; first glume 5.8-12.8 mm long, 1-4 mm wide between the keels, the folded under portion encompassing the keels and margins 0.2-1.1 mm wide, second glume 5.3-11.3 mm long, glabrous to villous especially on the basal half and margins; sterile lemma 3.6-9.0 mm; fertile lemma 4.0-10.0 mm long; palea inconspicuous; anthers 2.3-5.5 mm long; lodicules ca. 0.6 mm long. Sessile hermaphrodite spikelets long ciliate from the base to entirely glabrous, with a callus 0.3-2.6 mm long; first glume 3.9-6 mm long; second glume 3.3-6.0 mm long, with a

distinct longitudinal groove, glabrous; sterile lemma 3.5-5 mm long, the fertile lemma 2.1-4.5 mm long, the awn 2.0-8.6 mm long; palea inconspicuous, ca. 0.1-0.6 mm long; lodicules ca. 0.5 mm long. Fruit ca. 3.0-5.0 mm long (Fig. 2.5).

Leaves in cross-section with generally 3 sizes of bundles: the largest and midsize bundles with bundle caps on both the adaxial and abaxial sides and spanning the thickness of the leaf, the largest with conspicuously large vessels, the midsize bundles in sets of 2-5 intercalated between each pair of large bundles, without conspicuously large vessels, the smallest bundles intercalated in sets of 1-2 between each pair of midsize bundles, these with a bundle cap only on the abaxial side, spanning only the abaxial half of the leaf thickness, the other half being spanned by the bulliform cells. Bulliform cells in discrete groups of 2-7 in a single layer on the adaxial side of the lamina between the largest and midsize vascular bundle pairs. Both surfaces of the lamina with bicellular microhairs and often also with hooked prickles grading into straight unicellular trichomes sometimes to ca. 1 mm long, the bases of the larger trichomes inflated. Abaxial surface of the lamina densely papillate, with papillae to 20 µm long and 14 µm wide; bicellular microhairs 30.1-34.3 µm long with

their basal cell 12.5-16.3 µm long and their distal cell ca. 18 µm long; trichomes and prickles (when present) costal. Adaxial surface of the lamina not densely papillate, with bicellular microhairs more common than on the abaxial surface; the bicellular microhairs 23.8-41.5 µm long with their distal cell 11.4-17 µm long and their basal cell 10.8-24 µm long; trichomes and prickles costal but the microhairs both costal and intercostal; silica bodies dumbbell to 4-leaf-clover-shaped, often occuring in lines in contiguous cells in the costal region.

Phenology. Flowering and fruiting from November to June, peaking in late March.

Distribution and habitat. *Agenium leptocladum* grows in the open savannas and grasslands of South America. It is known from cerrado (sensu stricto) as well as the various types of cerrado (sensu lato) known as, campo sujo, campo limpo, and rarely campo rupestre. It ranges between 12.83° and 28.40° S latitude and 57.80° and 41.40° W longitude and from 61-1320 m in elevation (Fig. 2-6). The habitat is characterized by the following environmental variable extrapolations from the GIS described in Chapter 4: the percentage of possible sunshine hours that are actually sunny in Jan. 38-67%, Feb. 38-68%, Mar. 43-67%, Apr. 46-67%, May 48-81%, Jun. 40-86%, Jul. 51-86%, Aug. 49-87%, Sep. 10-

65%, Oct. 41-62%, Nov. 36-68%, Dec. 31-70%; mean monthly precipitation in Jan. 115-347 mm, Feb. 101-266 mm, Mar. 90-289 mm, Apr. 50-197 mm, May 16-161 mm, Jun. 2-140 mm, Jul. 3-94 mm, Aug. 5-111 mm, Sep. 21-142 mm, Oct. 98-197 mm, Nov. 86-270 mm, Dec. 117-350 mm; mean annual precipitation 1225-2178 mm; mean monthly temperature in Jan. 18.9-27.1° C, Feb. 19.8-27.3° C, Mar. 17.8-26.2° C, Apr. 15.7-27.2° C, May 12.7-25.3° C, Jun. 11.7-24.4° C, Jul. 12.4-24.4° C, Aug. 12.9-25.4° C, Sep. 13.8-28.2° C, Oct. 15.7-27.3° C, Nov. 17-27.3° C, Dec. 18.9-26.2° C; mean annual temperature 17.1-23.3° C; surface albedo in Oct. 11%-32%; generalized vegetation index (GVI) in Jan. 1990 129-157, Jul. 1990 116-145; percentage of sand in the top 1 m of soil 13-89%; percentage of silt in the top 1 m of soil 4-31%; percentage of clay in the top 1 m of soil 5-76%. The following environmental measurements were taken directly from soil samples taken with every Guala and Filgueiras collection (listed below): pH in H_2O 4.3-6.07; pH in N KCl 3.6-5.3; Al 0-2.05 Me/100 cm^3; Ca+Mg 0.09-1.48 Me/100g; P 0.6-4.3 ppm; K 8.5-95 ppm; organic matter 0.54-4.85%; Ca 0.07-1.07 Me/100g; coarse sand 4-34%; fine sand 12-86%; Sand (coarse+fine) 22-98%; Silt 0-43%; Clay 2-65%; hue of soil wet 2.5Y and 5-10YR dry 2.5Y, 5-10YR and 10R; color value of soil wet 2.5-6.5,

dry 3-7; chroma of soil wet 1-4, dry 1-6; bulk density 0.73-1.46 g/cm^3.

Additional specimens examined. ARGENTINA. Corrientes: Concepción, Pasture along the S side of Rt. 6, 6.5 km east of the Santa Rosa turnoff, 23 Feb. 1994, Guala 1623 (FLAS, IBGE, SI, US); Grasslands, Rincon de Luna, 26 Feb. 1961, Pederson 5807 (A, BAA); Estancia Buena Vista, 21 Feb. 1972 Pederson 10067 (AA, BR, CTES, MO, NY, UC); Concepción, 31 Dec. 1972, Pederson 13483 (AA, MO, NY). Misiones: San Ignacio, Jan. 1964, Crovetto 9849 (BAA) San Ignacio, Mar. 1952, Pederson 8253 (BAA).

BOLIVIA. Sara, Santa Cruz, 20 Mar. 1928, Steinbach 7939 (GH).

BRAZIL. Serra do Sihabiara, Dusén 273 (W). Distrito Federal: Anapolis Rd., 31 km from Brasilia, 23 Feb. 1965, Clayton 4806 (NY); 22 Apr. 1979, Brasilia, Ferreira s.n. (BM); Brasilia, Lago Norte, 19 Jan. 1981, Filgueiras 816 (MO); Brasilia, ARIE Capetinga, 8 Mar. 1994, Filgueiras 2903 (FLAS, IBGE, SI, SP, US); Brasilia, ARIE Capetinga, 8 Mar. 1994, Filgueiras 2905 (FLAS, IBGE, SI, SP, US); Chacara Baru, in the Quebrada dos Guimarans area. 8 Mar. 1994, Filgueiras 2906 (FLAS, IBGE, SI, SP, US); Reserva Aguas Emendadas, 11 Mar. 1994, Filgueiras 2912 (FLAS, IBGE, SI, SP, US); Filgueiras 2913 (FLAS, IBGE, SI, SP, US); 18 km

west of the Goias/Distrito Federal border, 11 Mar. 1994, Filgueiras 2914 (FLAS, IBGE, SI, SP, US); BR-020 at km 39, 11 Mar. 1994, Filgueiras 2915 (FLAS, IBGE, SI, SP, US); Reserva Ecológica do IBGE, 3 Apr. 1994, Filgueiras 2944 (FLAS, IBGE, SI, SP, US); Bacia do Rio São Bartolomeu, 9 June 1980, Heringer 5037 (LISC); Taguatinga, Córrego Cava do Reino, 8 Apr. 1981, Heringer 6754 (MO); Bacia do Rio São Bartolomeu, 22 Apr. 1981, Heringer 6827 (MO); Estação Experimental do Instituto Central de Biologia, Universidade de Brasília, 10 Apr. 1968, Lima 154a (NY); 10 Apr. 1968, Lima 176 (US); May 1968, Lima 225 (NY). Goiás: 7 km by road S of São João da Alliança, 22 Mar. 1973, Anderson 7666 (MO, NY); Rio Cristal, 44 km by Rd. SE of Cristalina, 6 April 1973, Anderson 8279 (MO, NY); 16 May 1973, Anderson 10303 (CTES, MO, NY, TAES); 15 miles N of Corumbá de Goiás, 14 May 1973, Anderson 10400 (MO, NY, TAES); Goiânia, 20-22 Mar. 1930, Chase 11452 (GH, NY); Sao Gabriel, 20 Feb. 1992, Filgueiras 2036 (SI); 45 km SE of Cristalina, 10 Mar. 1994, Filgueiras 2907 (FLAS, IBGE, SI, SP, US); Cristalina, 10 Mar. 1994, Filgueiras 2908 (FLAS, IBGE, SI, SP, US); top of hill SE of Cristalina, 10 Mar. 1994, Filgueiras 2910 (FLAS, IBGE, SI, SP, US); SE of Cristalina, Filgueiras 2911 (FLAS, IBGE, SI, SP, US); Povoada JK, 13 Mar. 1994, Filgueiras 2918 (FLAS, IBGE, SI, SP, US); Parque Nacional das Emas, 20 Mar.

1994, Filgueiras 2924 (FLAS, IBGE, SI, SP, UFG, US); Parque Nacional das Emas, South, 21 Mar. 1994, Filgueiras 2926 (FLAS, IBGE, SI, SP, UFG, US); Parque Nacional das Emas South, 22 Mar. 1994, Filgueiras 2928 (FLAS, IBGE, SI, UFG, SP, US); Crominia, 23 Mar. 1994 Filgueiras 2930 (FLAS, IBGE, SI, UFG, SP, US); Corumbá de Goiás, Salto do Corumbá, Filgueiras 2931 (FLAS, IBGE, SI, SP, US); 2 km from Colcalzinho, Filgueiras 2933 (FLAS, IBGE, SI, SP, US); Sao Gabriel, 13 Mar. 1994, Filgueiras 2943 (FLAS, IBGE, SI, SP, US); Rio Paraná, 35 km N of Formosa, 30 Mar. 1966, Alto do Paraiso, Irwin 14242 (MO); Alto do Paraiso, 23 Mar. 1969, Irwin 24946 (MO). Mato Grosso: Serra do Roncador, 24 May 1966, Irwin 15945 (MO); Serra do Roncador, 1 June 1966, Irwin 16411 (MO, US); 8 km N of 12°54'S, 51°52'W, 10 Apr. 1968, Ratter 949 (NY). Mato Grosso do Sul: Terenos, Fazenda Modelo, Allem 2068 (MO); Xavantina, 15 July 1968, Argent 6452 (NY); Campo Grande, 12 Mar. 1901, Dusén 4085. Minas Gerais: Serra do Cipó, 28 Mar.-1 Apr. 1925, Chase 9228 (MO).Paraná: Serrinha, 6 Apr. 1914, Dusén 152 (MO); Jaguariaiva, 1 Apr. 1915, Dusén 16956 (GH); Balsa Nova, Serra de São Luiz, 14 Jan. 1965, Smith 14413 (MO); Balsa Nova, Fazenda Cajurú, 18 Jan. 1965, Smith 14800 (NY). Rio Grande do Sul: Tamanduá, 14 Mar. 1968, Hatschbach 18717 (MO, UC).

PARAGUAY. Cordillera de Mobutobi, Mar. 1881, Balansa 2982 (W); San Luis, Nov. 1908, Fiebrig 5196 (BAA); Cordillera de Altos, 1900, Hassler 3760 (GH, NY, W); Caaguazú, 1905, Hassler 9270 (NY, UC, W); Ypacaray, 1913, Hassler 12427 (GH, MO, NY, UC).

2. *Agenium majus* Pilger, Feddes Repertorium Specierum Novarum Regni Vegetabilis 43: 82. 1938. TYPE: Paraguay, in regione fluminis Alto Parana, 1909-1910, K. Fiebrig Plantae Paraguayenses 6418, (holotype, SI!).

Heteropogon villosus Nees var. *dactyloides* Hackel subvar. *riedelianus* Hackel, in Martius, Flora Brasiliensis. 2: 270. 1883. *Andropogon neesii* Kunth var. *dactyloides* Hackel subvar. *riedelianus* Hackel, Monographie Phanerogamarum 7: 582. 1889. *Andropogon villosus* (Nees) Ekman var. *dactyloides* Hackel subvar. *riedelianus* (Hackel) Henrard, Mededeelingen van het Botanisch Museum en Herbarium van Rijks Universiteit te Utrecht 40: 44. 1921. TYPE: Riedel s.n. (holotype, W!).

Figure 2-5. *Agenium leptocladum*. A. Habit. Bar equals 1 cm. B. Spikelet pair. Bar equals 1 mm. C. Dissection of pedicellate staminate spikelet: clockwise from bottom; first glume, three stamens, sterile lemma, lodicule, palea, lodicule, fertile lemma, second glume with callus attached. Bar equals 1 mm. D. Dissection of sessile fertile hermaphrodite spikelet. Left to right: lodicule, gynoceum, lodicule, palea, fertile lemma (awn truncated), sterile lemma, second glume, first glume (stamens omitted). Bar equals 1 mm.

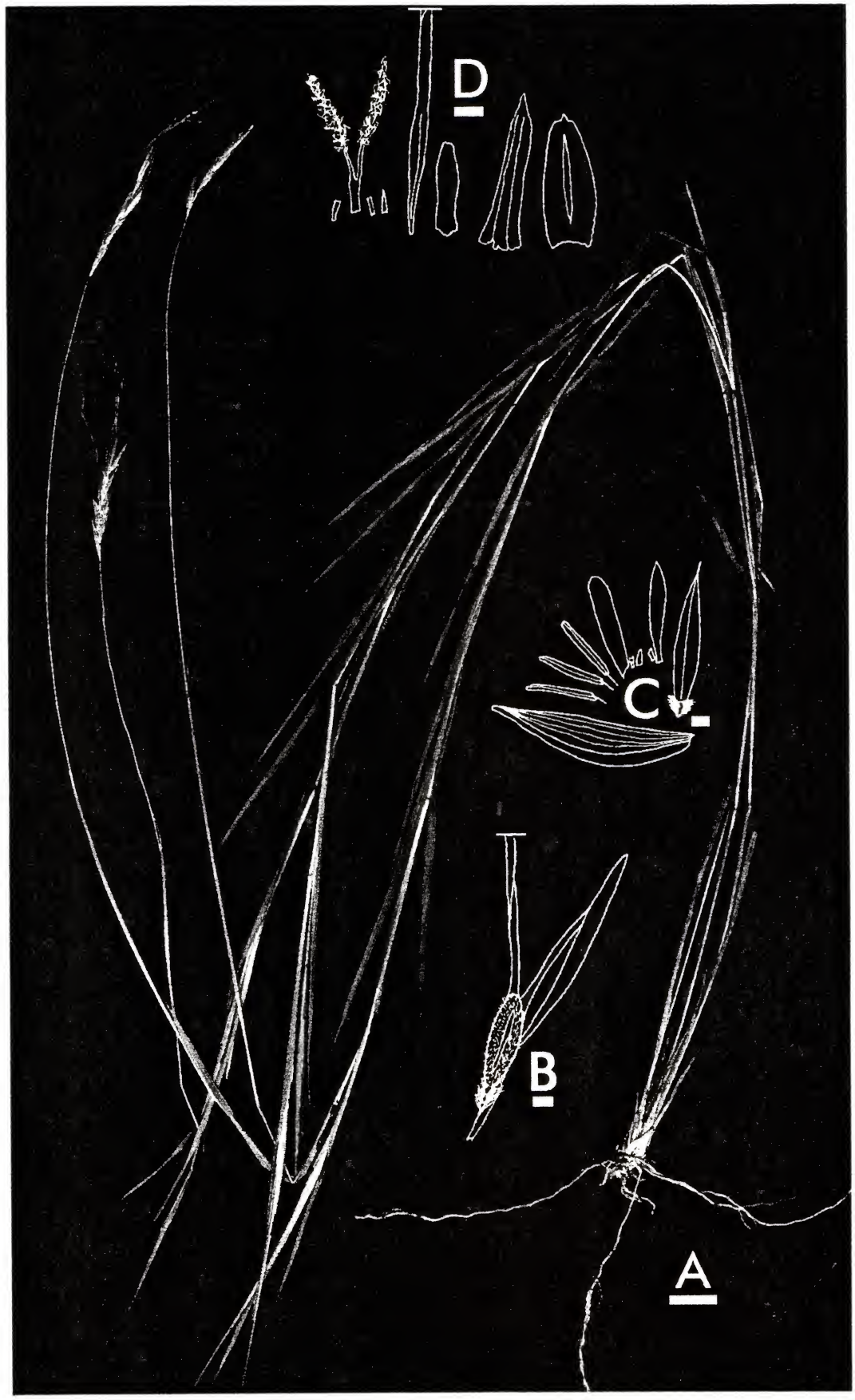

D
C
B
A

Figure 2-6. Distribution of *Agenium leptocladum*.

N
10°
20°
30°
40°
80°
70°
60°
50°
40°

Heteropogon villosus Nees var. *dactyloides* Hackel subvar. *selloanus* Hackel in Martius, Flora Brasiliensis. 2: 270. 1883. *Andropogon neesii* Kunth var. *dactyloides* Hackel subvar. *selloanus* Hackel, Monographie Phanerogamarum 7: 582. 1889. *Andropogon villosus* (Nees) Ekman var. *dactyloides* Hackel subvar. *selloanus* (Hackel) Henrard, Mededeelingen van het Botanisch Museum en Herbarium van Rijks Universiteit te Utrecht 40: 44. 1921. TYPE: Sello s.n. (holotype, W!).

Andropogon neesii Kunth var. *dactyloides* Hackel subvar. *paraguayensis* Hackel, Monographie Phanerogamarum VII. 1889. *Andropogon villosus* (Nees) Ekman var. *dactyloides* Hackel subvar. *paraguayensis* (Hackel) Henrard, in Mededeelingen van het Botanisch Museum en Herbarium van Rijks Universiteit te Utrecht 40: 44. 1921. TYPE: Balansa 223. (holotype, P).

Caespitose perennial. Rhizomes short. Bud scales often white-wooly, becoming stramineous. Culms erect, glabrous to short pubescent, branching near the base or not at all, 103-203 cm, the lower nodes 3-5.4 mm wide, villous. Leaves with their blades longer than the sheaths, short pubescent to long antorsely pilose; lamina ca. 20.5-78 cm

long, 3.8-8.2 mm wide, narrowly lanceolate, with a very prominent midvein, the margins minutely antorsely scabrous; ligule adaxially shiny brownish red, 0.8-3 mm long, truncate to dome-shaped, minutely fringed or smooth. Inflorescence a compound digitate panicle of 3-11 racemose segments; pedicel of the lowest segment 5-15 mm long, and each raceme 4.2-7.9 cm long, with 10-20 spikelet pairs; spikelets in the basal portion homogamous staminate; rachis segments between the basal homogamous spikelet pairs to 4 mm, those between the fertile pairs 0.3-4 mm. Sessile staminate spikelets with a callus ca. 1 mm long, obliquely attached; first glume 11.2-15.1 mm long, the abaxial surface glabrous to minutely papillate or rarely weakly glabrescent; second glume 9-12.3 mm long, completely or nearly symmetrical, less indurate than the first glume, glabrous; sterile lemma 7.2-10 mm long; fertile lemma 6-7.8 mm long; palea to 4.7 mm long; anthers ca. 3 mm long; lodicules ca. 0.8 mm long. Pedicellate staminate spikelets generally resembling the sessile staminate spikelets, on a pedicel 1.3-4.2 mm long, with the callus ca. 1 mm long; first glume 10.4-15.1 mm long, 2.2-4 mm wide between the keels, the folded under portion encompassing the keels and margins 0.4-1.3 mm wide; second glume 8.7-9.3 mm long, glabrous or rarely weakly glabrescent, the margin of the keels short to long scabrous;

sterile lemma 7.2-8.2 mm; fertile lemma 6-7.2 mm long; palea 3-4.7 mm long; stamens 3, the anthers ca. 2.9 mm long; lodicules 0.6-1 mm long. Sessile hermaphrodite spikelets, with a callus 0.9-2.7 mm long, its base long antorsely straight ciliate; first glume 6.1-7.3 mm long; second glume 7-7.5 mm long; sterile lemma 5-6 mm long; fertile lemma 5-6.1 mm long, the awn 6-9.5 cm; palea 3-4 mm long; lodicules 0.6-0.8 mm long, cuneate. Diaspore composed of the entire hermaphrodite spikelet with its callus, its awn and its attached fertile lemma deciduous upon dispersal. The fruit a caryopsis, ca. 6-7.5 mm long, with a longitudinal groove (Fig. 2-7).

Leaves in cross-section with generally 3 sizes of bundles; all with bundle caps on both the adaxial and abaxial sides; the larger 2 sizes spanning the thickness of the leaf and with their adaxial bundle caps slightly larger than their abaxial bundle caps, the smaller size bundles intercalated between the larger and spanning the thickness of the mesophyll between the interior surface of the bulliform cells and the abaxial epidermis, their adaxial bundle caps smaller than or equal to their abaxial bundle caps, the bulliform cells in discrete fan-shaped groups between the larger pairs of bundles, sometimes also in groups of small equally sized cells over the adaxial bundle

cap of the midsize bundles. Both surfaces of the lamina with bicellular microhairs and often also with hooked prickles grading into straight unicellular trichomes sometimes to 5.3 mm long, the bases of the larger trichomes inflated. Abaxial surface of the lamina not papillate or with a few papillae in the costal areas, bicellular microhairs present primarily intercostally, 46.3-58.6 µm long with their basal cell 17-21.1 µm long and their distal cell 27.6-41.6 µm long; trichomes and prickles (when present) costal. Adaxial surface of the lamina not papillate, but commonly with prickles at the costal edges, with bicellular microhairs less common than on the abaxial surface; bicellular microhairs 42.6-57.1 µm long with their distal cell 14.5-18.8 µm long and their basal cell 24.1-39.8 µm long; silica bodies often dumbbell to 4-leaf-clover-shaped with the latter being more common in this species than the others, generally in specific files or sets of files of cells in lines in contiguous cells in the costal region but tending not to be in contiguous cells in a file.

Phenology. This species blooms from November to March and fruits into June.

Distribution and Habitat. *Agenium majus* is known from cerrados of eastern Paraguay and western Brazil (Fig. 2-8). The habitat is characterized by the following environmental

variable extrapolations from the GIS described in Chapter 4: the percentage of possible sunshine hours that are actually sunny in Jan. 52-61%, Feb. 55-64%, Mar. 60-65%, Apr. 64-67%, May 62-67%, Jun. 56-67%, Jul. 62-71%, Aug. 64-71%, Sep. 52-60%, Oct. 56-62%, Nov. 60-66%, Dec. 51-64%; mean monthly precipitation in Jan. 158-210 mm, Feb. 127-216 mm, Mar. 110-141 mm, Apr. 101-127 mm, May 95-129 mm, Jun. 40-112 mm, Jul. 34-58 mm, Aug. 29-87 mm, Sep. 67-139 mm, Oct. 117-173 mm, Nov. 83-170 mm, Dec. 152-227 mm; mean annual precipitation 1421-1683 mm; mean monthly temperature in Jan. 23.7-26.5° C, Feb. 23-26° C, Mar. 21.9-25.7° C, Apr. 19.6-24.2° C, May 16.6-22.5° C, Jun. 15.1-21.7° C, Jul. 15-22.1° C, Aug. 16.4-22.1° C, Sep. 18.5-23.3° C, Oct. 20.4-25.5° C, Nov. 22-27.1° C, Dec. 23.4-25.8° C; mean annual temperature 21.9-23° C; surface albedo in Oct. 15%-16%; generalized vegetation index (GVI) in Jan. 1990 134-158, Jul. 1990 132-149; elevation 205-549 m; percentage of sand in the top 1 m of soil 13-89%; percentage of silt in the top 1 m of soil 4-14%; percentage of clay in the top 1 m of soil 7-76%.

Additional specimens examined. BRAZIL. Mato Grosso: Campo Grande, brushy campo, 7-11 Feb. 1930, Chase 10838 (MO); Campo Grande, W. of Campo Terenos Rd., 16 July 1966 Goodland 292 (MO).

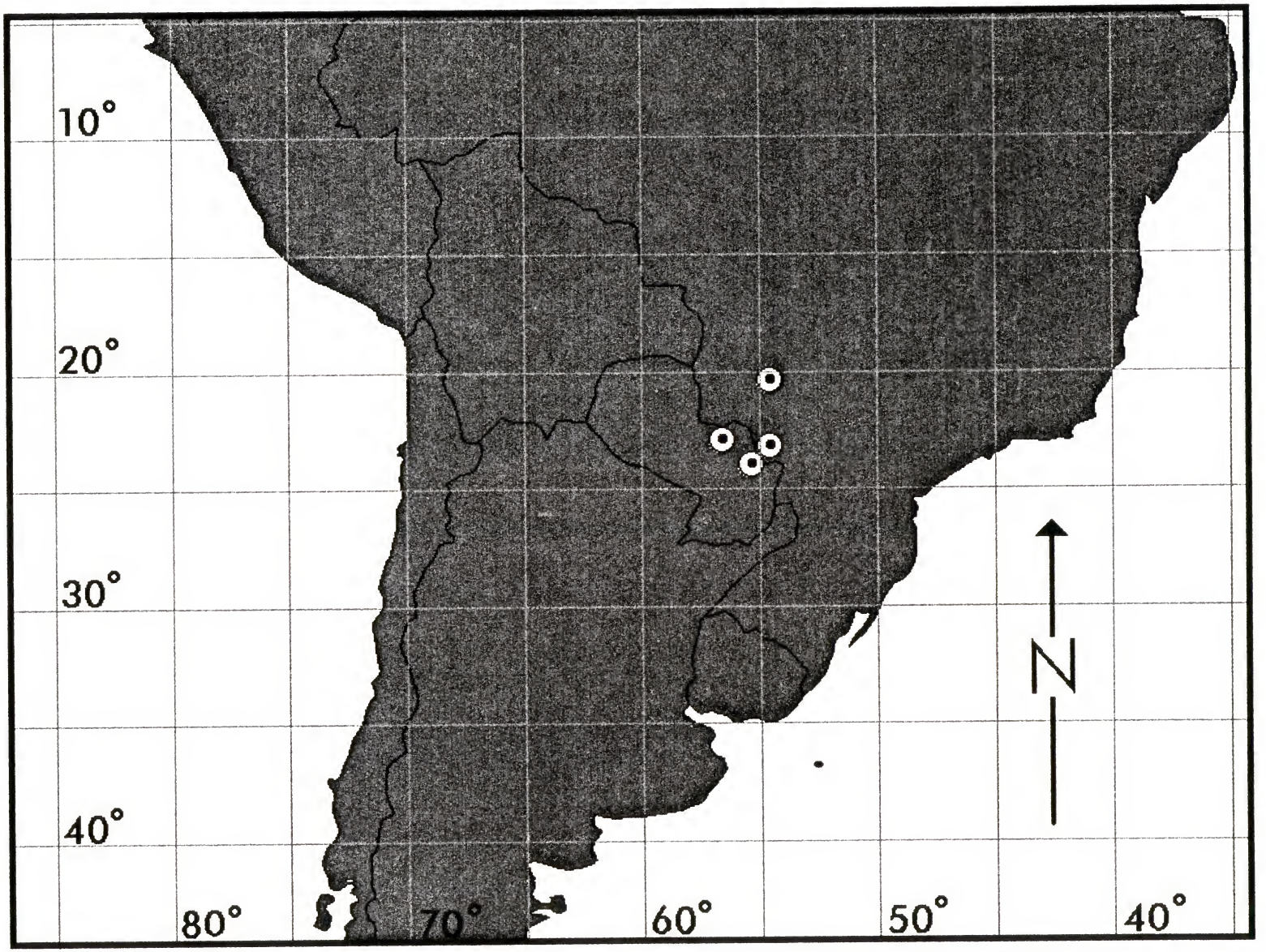
PARAGUAY. Vicinity of Igatimi, Nov. 1900, Hassler 5532 (NY, UC, W); Vicinity of Caaguazu, Mar. 1905, Hassler 9195 (NY, UC, W); Sierra de Amambay, Oct. 1912/13, Hassler 11386 (NY, W); Amambay, Oct. 1912/13, Hassler 11386 (MO, UC); Caaguazu, Estancia Primera, Feb. 1932, Jorgensen 4786 (MO, US); Estancia Primera, May 1927, Rojas 5152 (BAA).

3. *Agenium villosum* (Nees) Pilger, Repertorium Specierum Novarum Regni Vegetabilis 43: 82. 1938. *Heteropogon villosus* Nees, Flora Brasiliensis seu Enumeratio Plantarum 2: 362. 1829. *Andropogon neesii* Kunth *non* Trinius, Enumeratio Plantarum omnium hucusque cognitarum 1: 491. 1833. (Later homonym of *Andropogon neesii* Trinius = *Schizachyrium tenerum* Nees). *Heteropogon villosus* Nees var. *genuinus* Hackel subvar. *typicus* Hackel in Martius, Flora Brasiliensis. Vol 2: 270. 1883. *Andropogon neesii* Kunth var. *genuinus* Hackel subvar. *typicus* Hackel, Monographie Phanerogamarum 7: 582. 1889. *Andropogon villosus* (Nees) Ekman *non* Lam., Thunb., Gilib. (Later homonym of *Andropogon villosus* Lam., *A. villosus* Thunb., and *A. villosus* Gilib.) Arkiv för Botanik utgivet av K. Svenska Vetenskapsakademien 11: 9. 1912.

Figure 2-7. *Agenium majus*. A. Habit. Bar equals 10 cm. B. Inflorescence. Bar equals 1 cm. C. Spikelet pair. Bar equals 1 mm. D. (top down) Dissection of pedicellate male spikelet with the first glume, palea and lodicules excised. Dissection of sessile fertile hermaphrodite spikelet: first glume, second glume, sterile lemma, fertile lemma, lodicule, gynoceum, lodicule, palea, (stamens omitted). Bar equals 1 mm.

B
C
A
D

Figure 2-8. Distribution of *Agenium majus*.


10°
20°
30°
40°
80°
70°
60°
50°
40°
N

TYPE: Brasilia australiori, Sellow s.n. (holotype, B?; isotype, W!).

Agenium nutans Nees in Lindley, An Introduction to the Natural System of Botany 447. 1836. *Andropogon agenium* Steudel, Synopsis plantarum glumacearum 1: 395. 1854. *Heteropogon villosus* Nees var. *apogynus* Hackel, Martius Flora Brasiliensis 2: 270. 1883. *Andropogon neesii* Kunth var. *apogynus* Hackel, Monographie Phanerogamarum 7: 582. 1889. *Andropogon villosus* forma apogyna (Hackel) Henrard, Mededeelingen van het Botanisch Museum en Herbarium van Rijks Universiteit te Utrecht 40: 44. 1921. TYPE: Hackel 639 (holotype, B, not seen, US Acc.#00156344 fragment from B!).

Heteropogon villosus Nees var. *genuinus* Hackel subvar. *gardneri* Hackel in Martius, Flora Brasiliensis. Vol 2: 270. 1883. *Andropogon neesii* Kunth var. *genuinus* Hackel subvar. *gardneri* Hackel, Monographie Phanerogamarum 7: 582. 1889. *Andropogon villosus* (Nees) Ekman var. *genuinus* Hackel subvar. *gardeneri* (Hackel) Henrard, Mededeelingen van het Botanisch Museum en Herbarium van Rijks Universiteit te Utrecht

40: 44. 1921. TYPE: Brasil, Goyaz, Gardner 4061 (holotype, W!; isotype, NY!).

Heteropogon villosus Nees var. *genuinus* Hackel subvar. *leianthus* Hackel, in Martius, Flora Brasiliensis. Vol 2: 270. 1883. *Andropogon neesii* Kunth var. *genuinus* Hackel subvar. *leianthus* Hackel, Monographie Phanerogamarum 7: 582. 1889. *Andropogon villosus* (Nees) Ekman subvar. *leianthus* (Hackel) Ekman, Arkiv för Botanik utgivet av K. Svenska Vetenskapsakademien 11: 9. 1912. TYPE: Brasil, Lagoa Santa. Warming s.n. (holotype, W!).

Heteropogon villosus Nees var. *genuinus* Hackel subvar. *leiophyllus* Hackel in Martius, Flora Brasiliensis. Vol 2: 270. 1883. *Andropogon neesii* Kunth var. *genuinus* Hackel subvar. *leiophyllus* Hackel, Monographie Phanerogamarum 7: 582. 1889. *Andropogon villosus* (Nees) Ekman var. *genuinus* Hackel subvar. leiophyllus (Hackel) Henrard, Mededeelingen van het Botanisch Museum en Herbarium van Rijks Universiteit te Utrecht 40: 44. 1921. TYPE: Brasil. Sellow s.n. (holotype, W!).

Strongly caespitose perennial. Rhizomes generally short and compact. Bud scales glabrate to grey-villous. Culms green to grey-green to yellow, sometimes branching, especially in the basal half of the culm, generally villous but becoming glabrous in the lower internodes, 10.5-146.4 cm from the base to the base of the inflorescence, the nodes 0.5-2.5 mm wide, puberulent to villous, becoming glabrous with age, the upper nodes often with a ring of hairs to ca. 5mm long. Leaves with their blades longer than their sheaths, sparsely hirsute to pilose; lamina 5.3-47 cm long, 1-8.4 mm wide, linear to lanceolate with a prominent midvein to 0.7 mm wide, the margins minutely antorsely scabrous; ligule a hyaline membrane, 0.6-1.5 mm long, truncate to weakly triangular with a scabrous to minutely fringed to erose or smooth margin. Inflorescence a compound digitate to subdigitate panicle of 2-14 racemose segments; pedicels ca. 1-8 mm long, each raceme 2.5-5 cm long with 6-18 spikelet pairs, spikelets in the basal portion homogamous staminate; rachis segments between the basal homogamous spikelet pairs to 0.4-2 mm, those between the fertile pairs 0.2-0.9 mm. Sessile staminate spikelets with a callus 0.1-0.25 mm long, usually somewhat obliquely attached; first glume 7-10.3 mm long, the abaxial surface glabrate to long villous; second glume 6.2-7.2 mm long, glabrate to villous

especially on the basal half and margins; sterile lemma 5.7-6 mm long; fertile lemma 4.9-5.2 mm long, hyaline; palea 0.8-1.7 mm long; anthers 3.9-4.1 mm long; lodicules 0.3-0.6 mm long. Pedicellate staminate spikelets with a pedicel 1-1.9 mm long, with the callus 0.1-0.3 mm long; first glume 6.9-10.7 mm long, ca. 1.1-3.2 mm wide between the keels, the folded under portion encompassing the keels and margins 0.1-0.4 mm wide; second glume 6-9.5 mm long, glabrate to villous especially on the basal half and margins; sterile lemma 5.5-8 mm, fertile lemma 4-7.3 mm long; palea 1-1.6 mm; anthers 3.8-4.1 mm long; lodicules 0.3-0.6 mm long. Sessile hermaphrodite spikelets, with a callus 0.7-1.4 mm long, long ciliate from the base; first glume 4.6-5.1 mm long; second glume 4.4-5.1 mm long, with a distinct longitudinal groove, glabrate to villous; sterile lemma 4.4-5 mm long, hyaline margined, villous; fertile lemma 3.1-4 mm long, its awn 2.1-6.2(7.5) cm long; palea 0.8-1.2 mm long; lodicules ca. 0.5-0.6 mm long. The caryopsis 1.9-3.0 mm long, with a longitudinal groove (Fig. 2-9).

Leaves in cross-section with generally 3 sizes of bundles: the largest and midsize bundles with bundle caps on both the adaxial and abaxial sides and spanning the thickness of the leaf, the largest with conspicuously large vessels, the small bundles in sets of 1-3 intercalated

between each pair of larger or larger and midsize bundles, spanning the thickness of the mesophyll between the interior surface of the bulliform cells and the abaxial epidermis, the large and midsize bundles with roughly equal bundle caps on both sides or the adaxial cap larger, the small bundles without a bundle cap on the adaxial side and usually with only ca. 1-8 fibers in the abaxial bundle cap. Bulliform cells in discrete groups of 2-7 in a single layer on the adaxial side of the lamina between the largest and midsize vascular bundle pairs. Both surfaces of the lamina with bicellular microhairs and often also with hooked prickles straight unicellular trichomes sometimes to ca. 1.5 mm long also present, the cell around the base of the bigger trichomes often inflated. Abaxial surface of the lamina with lines of evenly spaced papillae to 12 µm long and 30 µm wide, and wider than tall, bicellular microhairs 29.3-45.6 µm long with their basal cell 11.8-23 µm long and their distal cell 13.8-25.7 µm long; trichomes both on the edge of costae and intercostal; prickles (when present) costal. Adaxial surface of the lamina with very few if any papillae, with bicellular microhairs 34.9-42 µm long with their distal cell 16.9-21 µm long and their basal cell 16.5-21 µm long, trichomes intercostal and prickles costal but the microhairs primarily on the edges of the costae; silica bodies

dumbbell-shaped or rarely 4-leaf-clover-shaped, often occuring in lines in contiguous cells in the costal region. 2n=20, meiosis normal (*fide* T. Killeen, note on Killeen 2419).

Phenology. Flowering or fruiting essentially all year but the flowering is concentrated from January through April with the peak in February.

Distribution and Habitat. *Agenium villosum* grows in the open savannas and grasslands of South America. It occurs in cerrado, campo sujo, and campo limpo, and ranges generally between 7.38° and 34.55° S latitude and 63.25° and 45.67° W longitude and from 10-1188 m in elevation (Fig. 2-10). The habitat is characterized by the following environmental variable extrapolations from the GIS described in Chapter 4: the percentage of possible sunshine hours that are actually sunny in Jan. 36-74%, Feb. 37-73%, Mar. 37-69%, Apr. 45-67%, May 48-81%, Jun. 40-86%, Jul. 50-86%, Aug. 49-87%, Sep. 11-65%, Oct. 42-63%, Nov. 37-71%, Dec. 36-72%; mean monthly precipitation in Jan. 78-339 mm, Feb. 72-256 mm, Mar. 90-298 mm, Apr. 51-197 mm, May 18-164 mm, Jun. 4-189 mm, Jul. 4-140 m, Aug. 2-133 mm, Sep. 30-192 mm, Oct. 71-190 mm, Nov. 77-265 mm, Dec. 81-350 mm; mean annual precipitation 1074-2178 mm; mean monthly temperature in Jan. 15.1-28° C, Feb. 14.9-27.1° C, Mar. 15.3-25.8° C, Apr. 12.7-

25.6° C, May 11.1-25.2° C, Jun. 8.4-25.1° C, Jul. 8.4-25.2° C, Aug. 8.8-26.7° C, Sep. 10.8-27.8° C, Oct. 12.8-26.9° C, Nov. 14.6-27.3° C, Dec. 15.9-27° C; mean annual temperature 16.3-26° C; surface albedo in Oct. 11%-32%; generalized vegetation index (GVI) in Jan. 1990 126-156, Jul. 1990 116-163; percentage of sand in the top 1 m of soil 10-91%; percentage of silt in the top 1 m of soil 3-48%; percentage of clay in the top 1 m of soil 5-76%. The following environmental measurements were taken directly from soil samples taken with every Guala and Filgueiras collection (listed below): pH in H_2O 3.9-7; pH in N KCl 3.8-6.2; Al 0-1.22 Me/100g; Ca+Mg 0.45-35.83 Me/100g; P 1-17 ppm; K 31-225.3 ppm; organic matter 0.72-5.6%; Ca 0.36-29.58 Me/100g; coarse sand 2-32%; fine sand 13-81%; Sand(coarse+fine) 17-94%; Silt 0-34%; Clay 5-57%; hue of soil wet 5-10YR, dry 5-10YR and 10R; color value of soil wet 2.5-4, dry 2.5-6; chroma of soil wet 1-6, dry 1-5; bulk density 0.85-1.51 g/cm^3.

Additional specimens examined. ARGENTINA. Corrientes: Concepción, Estancia Millán, 27 Mar. 1975, Arbo 921 (US); Estancia El Ciervo, 24 Apr. 1968, Carnevalli 1091 (CTES); Estancia El Tobaco, 17 Apr. 1972, Carnevalli 3062 (BAA), CTES); Santa Rosa, 26 Dec. 1978, Crovetto 11275 (CTES); Empedrado, 22 Feb. 1994, Guala 1622 (FLAS, IBGE, SI, US);

Rincón de Luna, 10 Feb. 1963, Hernández 605 (CTES); San Miguel, San Miguel, 1 Feb. 1946, Ibarrola 1491 (MO); Loreto, 8 Jan. 1946, Ibarrola 4108 (BR, MO, US, W); San Miguel, 1 Feb. 1946, Ibarrola 4191 (US); Ituzaingó, Estancia del Plata, Neiff 1329 (CTES); Mburucuyá, Loma Alta, 4 Jan. 1962, Parodi 6423 (A, TAES, US); "Estancia Garruchos", 29 Jan. 1951, Pedersen 965 (A, US); Estancia "Las Tres Marias", 2 Aug. 1954, Pederson 2753 (A, US); Saladas, Estancia "San Carlos", 26 Feb. 1970, Pedersen 9659 (NY, UC, US); Road to Garruchos, 5 Feb. 1972, Quarín 424 (CTES); 11 Feb. 1972, Quarín 509 (BAA, UC); Loreto, 8 Mar. 1974, Schinini 8454 (TAES); Santo Tomé, 8km E of Gobernador de Virasoro, 28 Jan. 1987, Schinini 25287 (CTES, MO, UC); 22km E del desvio a Ituzaingó, 24 June 1990, Schinini 26865 (A, MO). Entre Rios: Concordia, Salto Grande, 21 Sept. 1957, Boelke 4845 (SI); Federación, Salto Grande, 27 Nov. 1968, Burkart 27171 (US); 21, Sept. 1951, Cabrera 10796 (CTES); Gravel Cliffs above the río Uruguay, 5 Oct. 1978, Renvoize 2934 (NY, MO) Santa Ana, 21 Sept. 1978, Troncoso 2295 (US). Misiones: Apóstoles, Feb. 1961, Crovetto (BAA); Posadas, Bonpland, 8 Jan. 1908, Ekman 564 (US); San Ignacio, 18 Feb. 1994, Guala 1616 (FLAS, IBGE, SI, US); Apostoles, 19 Feb. 1994, Guala 1617 (FLAS, IBGE, SI, US); Gobernador de Virasoro, 20 Feb. 1994, Guala 1618 (FLAS, IBGE, SI, US); Road to Garruchas

from Gob. Virasoro, 20 Feb. 1994, Guala 1619 (FLAS, IBGE, SI, US); Road to Garruchas from Gob. Virasoro, 20 Feb. 1994, Guala 1620 (FLAS, IBGE, SI, US); Road to Garruchas from Gob. Virasoro, 20 Feb. 1994, Guala 1621 (FLAS, IBG E, SI, US); Candelaria, Arroyo San Juan, 16 Jan. 1966, Krapovickas 12046 (CTES, UC); 6 Aug. 1912, Lillo 12118 (W); Loreto, 19 Nov. 1951, Montes 12327 (US); Nacanguazú, 1 Apr. 1958, Montes 27581 (MO, NY); Gobernación de Misiones, 15 Jan. 1922, Parodi 4101 (US); Between Loreto and San Ignacio, 4 Jan. 1972, Quarin 157 (CTES); Santa Ana, Nov. 1912, Rodríguez 546 (BAA, GH, UC, US); Puerto Cazador, 9 Oct. 1947, Schwarz 4923 (NY); Cainguás, Jardín América, 27 Nov. 1948, Schwarz 6690 (US); Salto las Golondrinas, 18 Oct. 1975, Zuloaga 505 (CTES); San José, Cerro Ceferino, Apr. 1979, Zuloaga 887 (PRE, SI).

BOLIVIA. Meeled 1300 (W). Santa Cruz: Andreas Ibañez, Arubay, 18 Mar. 1989, Coimbra s.n. (NY); Santa Cruz, 4 Feb. 1994, Guala 1609 (FLAS, IBGE, SI, US); Santa Cruz, 4 Feb. 1994, Guala 1610 (FLAS, IBGE, SI, US); 2 km S of Concepción, 14 Feb. 1985, Killeen 854 (MO); Nuflo de Chavez, Estancia Viera, 23 Mar. 1987, Killeen 2419 (CTES, MO); 28 km SW of center of Santa Cruz, 27 Feb. 1988, Nee 36425 (MO, NY, US); 50 km S of Santa Cruz, 14 Mar. 1981, Renvoize 3945 (MO);

Sara, on the río Gwendú, 20 Mar. 1928, Steinbach 7939 (BM, GH, MO, NY).

BRAZIL. Serrinha, 3 Feb. 1916, Dusén 17664 (BR, GH); Glaziou 20146 (W); Pohl 1601 (W); Riedel s.n. (GH, NY, W); Sellow s.n. (BR). Distrito Federal: 3 km W of the Goiás/DF border along BR-020, 9 Apr. 1976, Davidse 12171 (MO, NY, PRE, TAES); Brasilia, Bacia do Rio São Bartolomeu, 7 Apr. 1980, Heringer 4249 (MO, US). Goiás: Crominia-Maripotaba, 14 Apr. 1988, BRASPEX 96 (MO, NY); Crominia-Maripotaba, 27 Apr. 1988, BRASPEX 195 (MO, NY); Goyandira, 26-27 Mar. 1930, Chase 11583 (GH); Cristalina, 10 Mar. 1994, Filgueiras 2908 (FLAS, IBGE, SI, US); Crominia, 23 Mar. 1994, Filgueiras 2930 (FLAS, IBGE, SI, US); Povoada JK, 13 Mar. 1994, Filgueiras 2918 (FLAS, IBGE, SI, US); Fazenda de Samarão, Glaziou 22363 , (BR, GH, W); Rio Paraná, 35 km N of Formosa, 30 Mar. 1966, Irwin 14241 (MO). Maranhão: Loreto, Fazenda Morros, Eiten 4413 (MO). Mato Grosso: Rio Brilhante, Rio Anhnadui, 23 Oct. 1970, Hatschbach 25096 (UC). Minas Gerais: S. Vicente, 25 Feb. 1951, Macedo 3205 (MO); 1847 Regnelli 1381, (W); Regnelli 1382 (W); campestre a serra, 15 dec. 1946, Macedo 847 (MO); Agua Limpa, 20 Feb. 1948, Swallen 9242 (UC). Paraná: Outskirts of Curitiba, 22 Jan. 1965, Clayton 4223 (NY); Castro, PR-11, 15 Mar. 1976, Davidse 11392 (MO); Jan. 1967, Dombrowski 2290 (CTES); Rio

Tabagy, 7 Jan. 1904, Dusén 3249 (MO, W); Jaguariaiva, 30 Dec. 1914, Dusén 16220 (MO); Arapoti, Rd. to Jaguariaiva, 17 Jan. 1965, Smith 14713 (NY); Araucária, 22 Jan. 1994, Filgueiras 2894 (FLAS, IBGE, SI, US); Rio Barigui, 26 Jan. 1975, Hatschbach 35820 (NY); Guarapuava, Fazenda Campo Real, 7 Feb. 1969, Hatschbach 21015 (NY, UC); 10 km E of Vila Velha, 15 Feb. 1973, Krapovickas 23281 (CTES); Curitiba, waste place on a hill, 27 Jan. 1966, Lindeman 417 (NY, W); Ponta Grossa, Estacão Experimental, 2 Feb. 1946, Swallen 8400 (US). Rio Grande do Sul: Jardim Botânico da FZB, 21 Sept. 1982, Bueno 3570 (CTES); São Francisco de Paula a Tainhas, 29 Jan. 1964, Burkhart 25055 (SI); Passo Fundo 27 km NW of Vacaria, 11 Mar. 1976, Davidse 11153 (MO); Loledade, Fazenda St. Thomé, Dec. 1910, Jürgens G392 (W); Porto Alegre, 23 Sept. 1946, Jürgens 33877 (SI); Fazenda Hortência, 29 Apr. 1974, Porto 811 (TAES); Bom Jesus; Fazenda B. Velho, 6 Jan. 1947, Rambo 35172 (MO); Furna do Tigre, near Itapoan, 19 Nov. 1949, Rambo 44437 (MO); Oct. 1932, Orth 855 (MO); Morro das Albertas, 28 Sept. 1949, Rambo 43630 (CTES, MO); Tupaceretà, Nov. 1934, Sanji 162 (BAA); Morro da Gloria, 25 Sept. 1971, Valls 1634 (TAES). Santa Catarina: Lajes, Estrada São Joaquim, 18 Feb. 1972, Pott 7658 (BAA); Lajes, 4 Feb. 1963, Reitz 6608 (NY, UC); 15 Jan. 1957, Smith 10047 (NY, US); Morro Pinheiro Sêco, 16

Mar. 1957, Smith 12219 (NY, UC, US); South of Painel, 19 Dec. 1971, Smith 15911 (GH, MO, UC). São Paulo: 18 Mar. 1857, Regnelli 1383 (W); Ypiranga, 19 Jan. 1908, Usteri 9608 (GH, NY); on Rio Grande, 1902, Wacket s.n. (W).

PARAGUAY. Jan. 1875, Balansa 221 (BR); Cerro Perón, Balansa 221b (US fragment from W, W); 24 Mar. 1876, Balansa 221c (W); Villa Loma, Jan. 1908/9, Fiebrig s.n. (GH, W); Cordillera de Altos, Feb 1903, Fiebrig 932 (GH, US, W); Between the río Apa & río Aquidaban, Oct. 1908/9, Fiebrig 4090 (GH, US, W); Amambay, Cero Cora National Park, 28 Feb. 1994, Guala 1624 (AS, FLAS, IBGE, US); Rio Apa, Dec. 1902, Hassler 8080 (GH, NY, UC, W); Caaguazú, March 1905, Hassler 9246 (MO, NY, UC, W); Sierra de Amambay, Dec. 1907/8, Hassler 9885 (NY, US, W); Dec. 1912/3, Hassler 11908 (US); Ypacaray, Mar. 1913, Hassler 12554 (GH, MO, NY, UC, US); Itupé, Jan. 1931, Jorgensen s.n. (BAA, CTES, MO, NY, US); Estancia Primera, Feb. 1932, Jorgensen 4783a (MO); Del Guairá, Borja, 11 Feb. 1953, Montes 16158 (US); Caballero, Jan. 1888-1890, Morong 423 (GH, MO, NY, UC, US); Misiones; 27 Jan. 1949, Ramirez 205 (BAA); San Ignacio, 27 Jan. 1949, Rosengurtt B-5587 (US); 16 Feb. 1950, Rosengurtt B-5782 (US).

URUGUAY. Dec. 1891, Arechavaleta 28 (US); Sierra de Halebrigo, Nov. 1922, Hauman s.n. Cerro Largo: Rio Negro,

Palleros, Dec. 1937, Rosengurtt B-2365 (UC, US). Lavalleja: Nico Pérez, 25 Nov. 1947, Herter 99776 (MO, US). Montevideo: Oct. 1937, Lombardo 2109 (BAA); Cerro de Montevideo, Oct. 1888, Arechavaleta 270 (W). Paysandú: Chapicuy, Sta. Sofia, 13 Nov. 1942, Rosengurtt B-4222 (US). Salto: Arapay, Sept. 1949, Herter 50910. Treinta y Tres: Quebrada de los Cuervos, 16 Dec. 1964, Brescia 3819 (US).

Unknown Locality: Monard 1829 (W).

Figure 2-9. *Agenium villosum*. A. Habit. Bar equals 1 cm. B. Dissection of sessile fertile hermaphrodite spikelet. Left to right: palea, lodicule, gynoecium, lodicule, fertile lemma (awn truncated), sterile lemma, second glume, first glume (stamens omitted). Bar equals 1 mm. C. Spikelet pair. Bar equals 1 mm. D. Dissection of pedicellate staminate spikelet: second glume, fertile lemma, stamen, lodicule, stamen, palea, lodicule, stamen, sterile lemma, first glume. Bar equals 1 mm.

B
C
A
D

Figure 2-10. Distribution of *Agenium villosum*.

10°
20°
30°
40°
80°
70°
60°
50°
40°
N

CHAPTER 3
A REVISION OF *HOMOZEUGOS*

Introduction

The genus *Homozeugos* is a member of the Andropogoneae (Poaceae), occurring in the savannas, grasslands and forests of central Africa. It is characterized by the large homomorphic spikelet pairs that give it its name. *Homozeugos eylesii* has been observed being eaten by both domesticated and wild ungulates and all members of the genus undoubtedly have contributed to the diet of the vast ungulate fauna of its native range as well as the great herds of domestic stock that now roam the region.

Homozeugos was first described by Stapf (1915) to accommodate his new species, *H. fragile*, as well as *H. huillense*, which had been described by Rendle (1899) as *Pollinia huillense*. Stapf (1917) went on to name another species, *H. gossweileri*, after the insatiable Portuguese collector of Angolan plants João Gossweiler, who first found it. *Homozeugos eylesii*, the most widespread and now best collected species remained undescribed for nearly 20 years. Hubbard (1936) published it in one of the many "Notes on

African Grasses" that have appeared in the Kew Bulletin over the years. The first real treatment of the genus, which included the publication of *H. katakton*, was done by another famous agrostologist from Kew, W.D. Clayton (1973), who clearly expressed the need for further collection and study in the genus. In the present investigation, I was able to collect specimens from throughout the range of the genus with the exception of Angola (where civil war prevented my work). The number of known collections was nearly doubled through my efforts. I have been able to use my collections, as well as those already in herbaria, to clarify the phylogenetic relationships among the species, describe a new species, and provide the first full monograph of the genus.

Materials and Methods

Herbarium specimens representing the known range of variation in *Homozeugos* were made from natural populations throughout much of its geographic range (see Figures 3-6, 3-8 & 3-10). A total of 63 sheets representing all known populations of *Homozeugos* were borrowed from BR, K, LISC, LISCJ, MO, NY, PRE, SRGH, UC and US. Other specimens at PRE and SRGH were measured on site. All available specimens were scored for the macro-morphological characters included in the descriptions below. At least five replicates of most

measurements were made per collection (when possible). Height was measured as the distance from the base of the culm where it enters the ground to the base of the inflorescence. Heights were measured in the field in my own collections and were taken from randomly selected individuals within the population. Transverse sections of leaves of all of my own collections were prepared and observed as described in Guala (1995). Specimens from the midportion of mature midculm leaves of all of my collections also were prepared as described by Guala (1995) for observation under the SEM. All samples were digitally photographed at 90X across their entire surface and then several representative photos from each side were taken at higher magnifications. These were saved as 1024 X 768 Tiff files and databased with the other morphological data.

Data sets were analyzed phylogenetically using ALLTREES with parsimony in PAUP* 4.0d60 *beta* as well as the ALLTREES Algorithm of PAUP 3.1.1 (Swofford 1991). The same results were obtained with both.

Phylogenetic Analyses

The original operational taxonomic units (OTUs) were 19 separate entities corresponding to populations or putative

meta-populations that appeared to be clearly homogeneous. Upon measurement of all characters it became clear that these OTUs fell into six diagnosable entities. There was overlap in the distribution of every character state within each of the entities and no individual or entity of individuals within a group could be explicitly described (or diagnosed) as distinct. These six diagnosable entities were used in the cladistic analysis of the ingroup.

The phylogenetic species concept (PSC) of Donoghue (1985), Mishler (1985), and Mishler & Brandon (1987) was employed in this study. The study is based on the assumption that recognizable evolutionary events occur at low taxonomic levels making species the minimum diagnosable phylogenetic units in an evolutionary hierarchy. This "history based" (Baum and Donoghue 1995) definition of species is, therefore, considered appropriate in this study. The theoretical pitfalls of applying the concept of monophyly at the species level are well publicized and an alternative PSC has been proposed to circumvent the problem (Nixon and Wheeler 1990, 1992, Davis and Nixon 1992, Davis 1993). This alternative PSC can be called "character based" because it relies only on the distribution of unpolarized characters. Thus, the inference is that lineage building cannot occur within a species, so a phenetic diagnosis is

the best that one can achieve. Because I used only characters with states that are discrete between OTUs and constant within them, and because I only lumped together local populations between which I could find no consistent differences, the grouping requirements for the alternative PSC are met for the designation of diagnosable entities (not species) in this study. However, as a ranking criterion for the species level, I believe that the original PSC (Donoghue 1985, Mishler 1985, Mishler & Brandon 1987) is much more informative and philosophically appealing for this type of study.

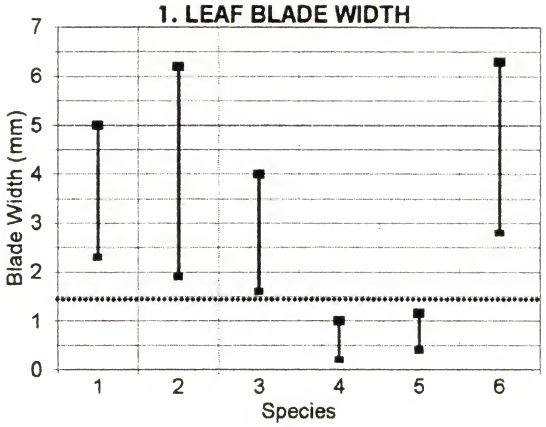
In the cladogram of Kellogg and Watson (1993), *Homozeugos* forms a well supported clade (by six synapomorphies: not defined in text) with *Trachypogon*. This clade is well supported in the molecular study presented in chapter 2 as well. Both studies also confirm that *Agenium* is sister to the *Homozeugos+Trachypogon* clade. The genus *Homozeugos* is the only member of the Andropogoneae to have truly homomorphic sessile and pedicellate spikelets. A few genera such as *Eulalia* Kunth and *Microstegium* Nees have sessile and pedicellate spikelets that are very similar to each other but are actually dimorphic in size (especially with respect to their paleas) within a pair. These two genera probably form a clade of their own not related to

Table 3-1. Table of characters used in the cladistic analyses.

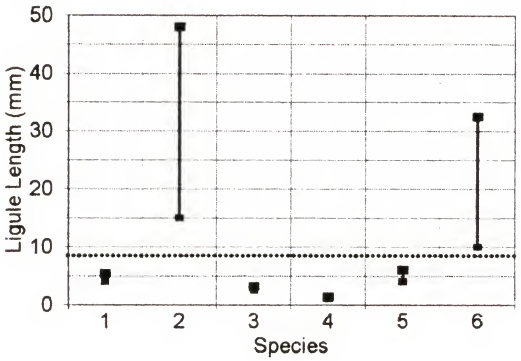
	State 0	State 1
1.	Leaf blades 0.2-1.15 mm wide.	Leaf blades 1.6-6.3 mm wide.
2.	Ligule of penultimate leaf 10-48 mm long.	Ligule of penultimate leaf 1-4 mm long.
3.	Awns 14-42 mm long.	Awns 45-83 mm long.
4.	Callus 0.8-2.3 mm long.	Callus 2.8-3 mm long. State (2) = Callus 3.2-4.2 mm long
5.	Sterile lemma 4.8-8 mm long.	Sterile lemma 8.5-10.2.
6.	Anthers 3-5.2 mm long.	Anthers 5.5-7.2 mm long.
7.	Prickles absent on the abaxial surface of the leaf blade	Prickles present on the abaxial surface of the leaf blade.
8.	Fertile lemma 3.5-7.7 mm long.	Fertile lemma 8-10 mm long.
9.	First glume 5.4-9 mm long.	First glume 9.3-11 mm long.
10.	Second glume 5.2-9.4 mm long.	Second glume 9.8-12 mm long.
11.	Lower culm nodes 1.9-3.7 mm long.	Lower culm nodes 3.8-4.5 mm long.
12.	Lamina absent from leaves.	Lamina present in leaves.
13.	Bulliform cells absent.	Bulliform cells present.
14.	Silica bodies with their long axis perpendicular to the leaf blade axis absent.	Silica bodies with their long axis perpendicular to the leaf blade axis present.
15.	Margins of the leaves antorsely scabrous.	Margins of the leaves entire.
16.	Distal cell of the adaxial microhairs 24.92-31.54 µm long.	Distal cell of the adaxial microhairs 15.87-24.48 µm long.
17.	Major vascular bundles of leaf blades not adaxially raised and abaxially domed.	Major vascular bundles of leaf blades adaxially raised with domed abaxial caps arching over them.

Figure 3-1. The ranges of states measured for quantitative characters numbered 1-6 and 8-9.

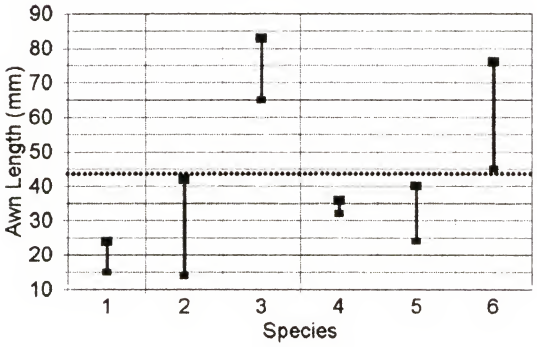
1. LEAF BLADE WIDTH



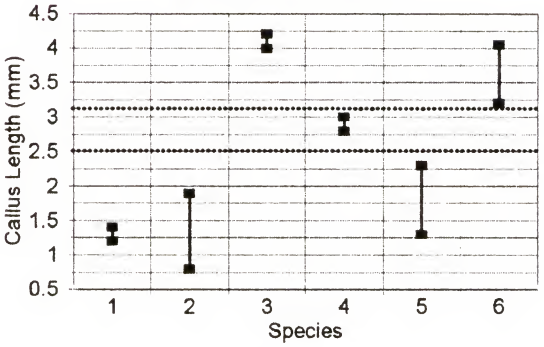
2. LIGULE OF PENULTIMATE LEAF



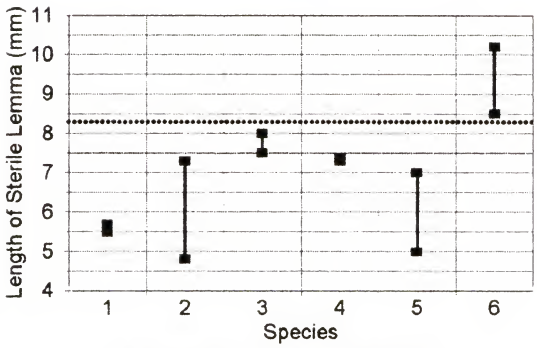
3. AWN LENGTH



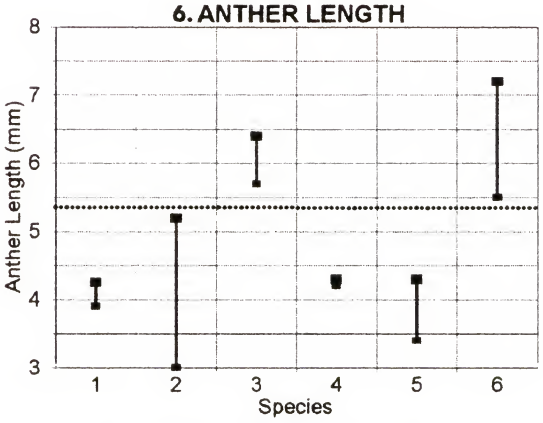
4. CALLUS LENGTH



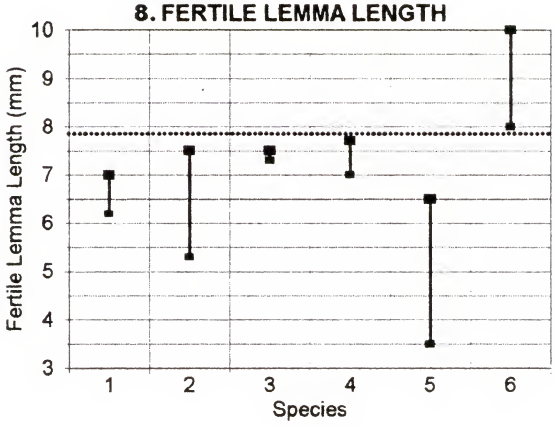
5. STERILE LEMMA LENGTH



6. ANTHER LENGTH



8. FERTILE LEMMA LENGTH



9. FIRST GLUME LENGTH

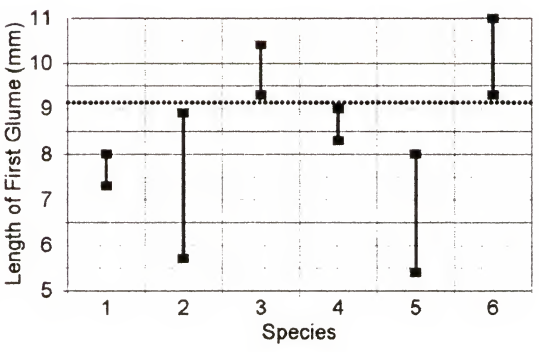
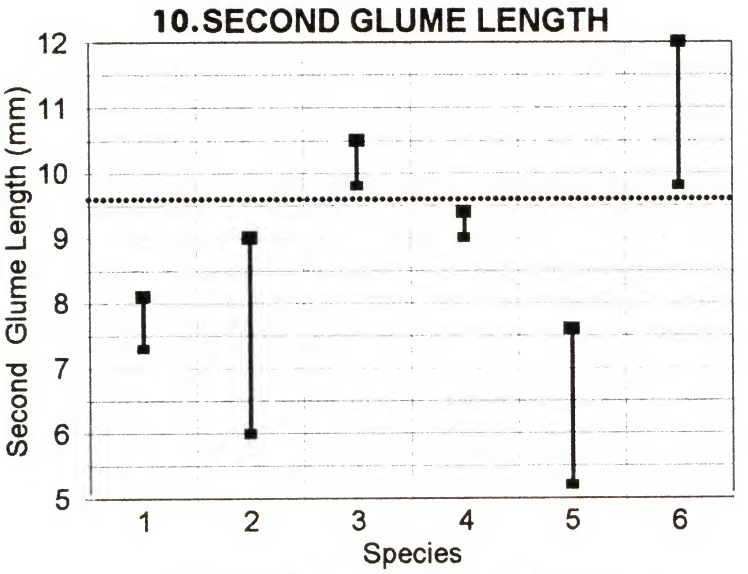
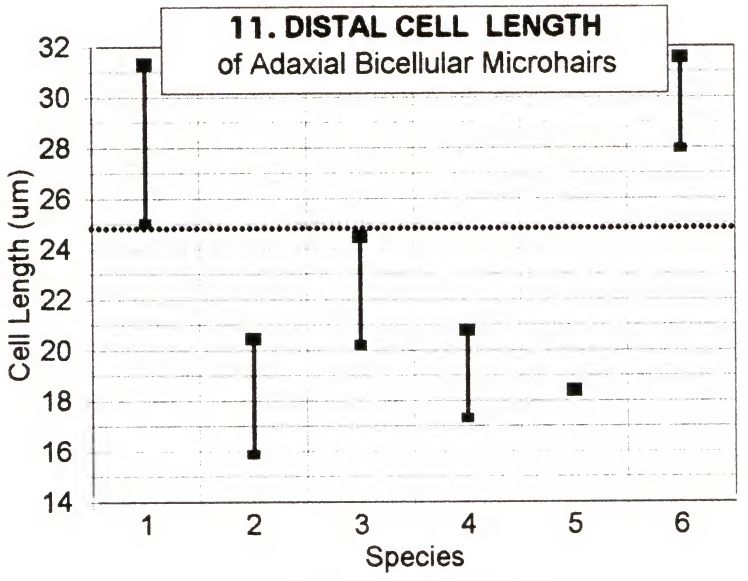


Figure 3-2. The ranges of states measured for quantitative characters numbered 10-11 and 16.


10.SECOND GLUME LENGTH
Second Glume Length (mm)
12
11
10
9
8
7
6
5
1
2
3
4
5
6
Species


11. DISTAL CELL LENGTH
of Adaxial Bicellular Microhairs
Cell Length (um)
32
30
28
26
24
22
20
18
16
14
1
2
3
4
5
6
Species

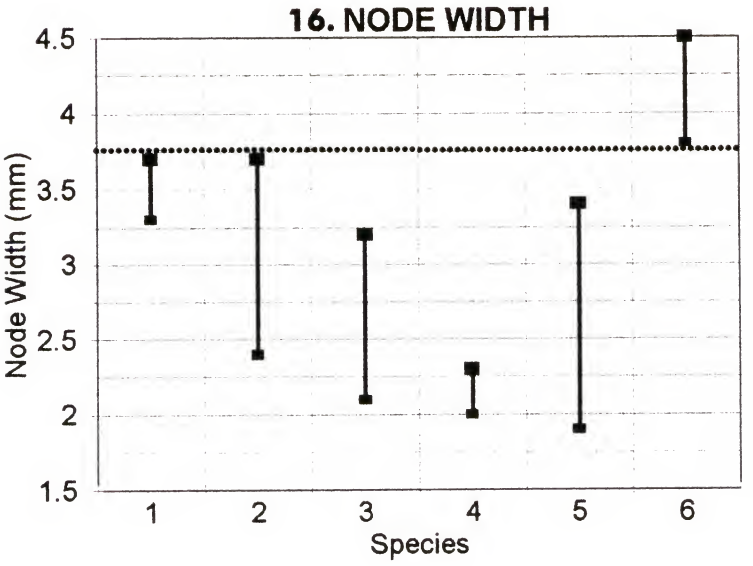
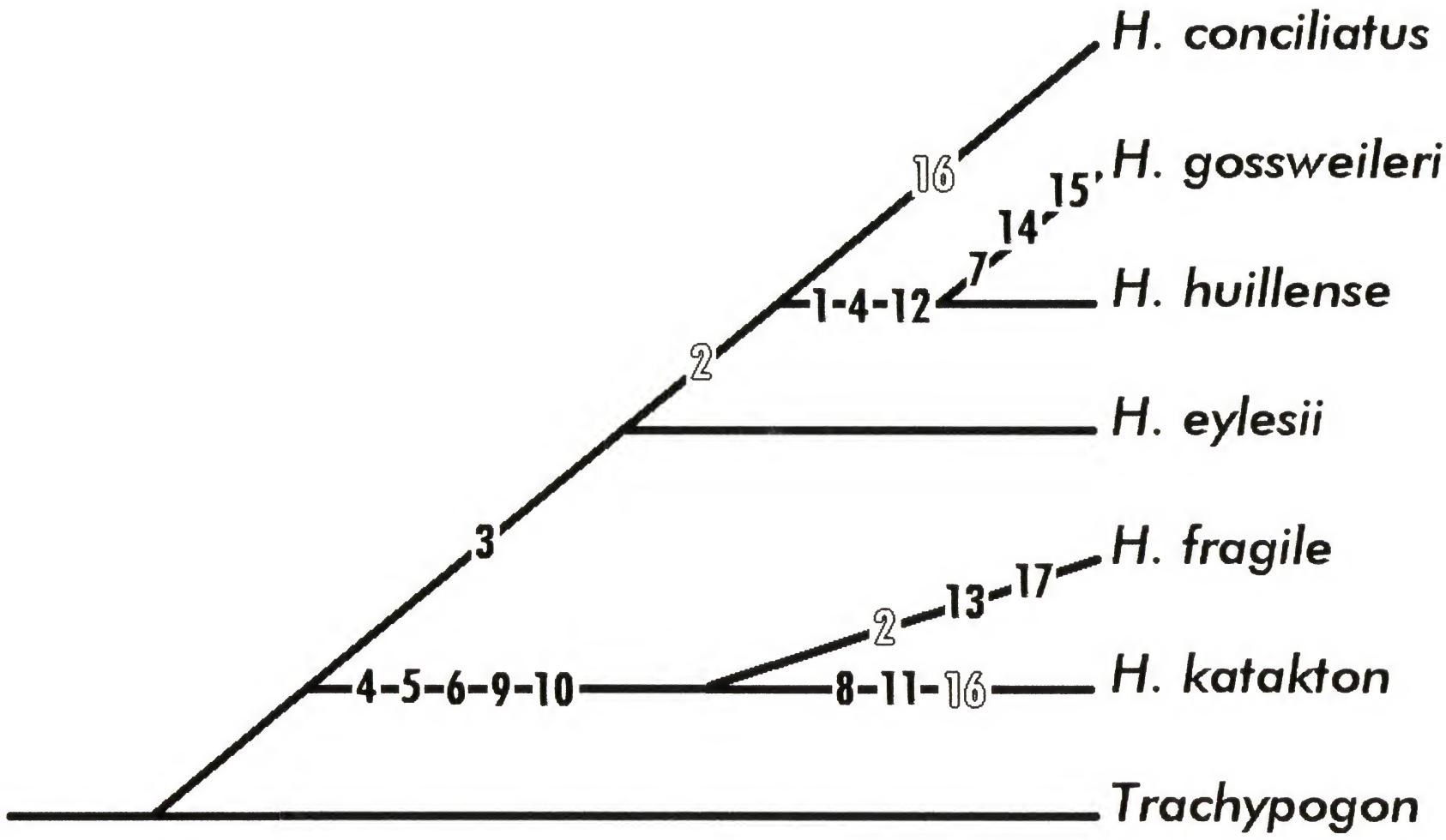

16. NODE WIDTH
Node Width (mm)
4.5
4
3.5
3
2.5
2
1.5
1
2
3
4
5
6
Species

Table 3-2. Character state distributions for the species of *Homozeugos* and the outgroup:(*Trachypogon*).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
H. conciliatus	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0
H. eylesii	1	1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0
H. fragile	1	0	1	1	1	1	1	0	1	1	0	1	0	0	0	0	1
H. gossweileri	0	0	0	0	0	0	0	0	0	0	0	0	?	1	1	0	0
H. huillense	0	0	0	0	0	0	1	0	0	0	0	0	?	0	0	0	0
H. katakton	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0
Trachypogon	?	1	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0

Figure 3-3. Cladogram of *Homozeugos*. Tree Statistics: 17 Characters, 20 steps, CI = 0.9, RI = 0.83, RC = 0.75. Numbers refer to characters in Table 3-1 and Figure 3-2. Homoplasious characters are represented by white numbers.


H. conciliatus
H. gossweileri
H. huillense
H. eylesii
H. fragile
H. katakton
Trachypogon
16
15
14
7
1-4-12
2
3
2
13
17
4-5-6-9-10
8-11-16

Homozeugos (*fide* Kellogg and Watson 1993). Given that both *Agenium* and *Trachypogon* have dimorphic spikelets, outgroup analysis suggests that the homomorphy of the spikelets is a clear synapomorphy for *Homozeugos* as are the fragile rachis of the raceme and the pungent callus although the latter two characters are common in the Andropogoneae. Clayton (1972) also found *Homozeugos* to be in an isolated position in his Principle Component Analysis (PCA) of the awned Andropogoneae.

Characters. A large number of characters including length of all major parts and appendages were originally measured. Hair morphology and density as well as surface texture and morphology were also measured. The characters in Figure 3-1 are those that showed informative distributions among the diagnosable entities and were subsequently used in the cladistic analyses. Because many of the characters are fundamentally quantitative, the delimitation of states became an issue in the study (see Stevens 1991). Character states were delimited only where a gap in the measured distribution of the character was recorded. Consideration of the distribution of measurements within taxa was also taken into account and characters states were defined based on distributions that appeared to show a true discontinuity rather than a merely incidental

gap. The measured ranges for quantitative characters used in this study are provided in Figures 3-2 and 3-3.

Discussion

The monophyly of the *Trachypogon+Homozeugos+Agenium* clade and the sister group relationship of the *Trachypogon+Homozeugos* clade and *Agenium* as well as the monophyly of *Homozeugos* are supported by both morphology (Kellogg and Watson 1993) and ITS sequences (Chapter 2). Within *Homozeugos*, the cladistic analysis shows that *H. katakton* and *H. fragile* form a well supported clade and the rest of the species are included in a clade supported by the presence of short awns. The characters supporting the *H. fragile+H. katakton* clade are all based on the length of various spikelet components. While there is no *a priori* reason that these should be correlated since flower part sizes vary widely with relation to each other in grasses, one can imagine a genetically simple, developmental shift producing flowers that are large in all respects. To test the effect of this, I re-analyzed the data with the five characters supporting this clade weighted as 0.2. Thus, as a group, they had the same weight as any other individual character. The results in this re-analysis were unchanged

(Figure 3-3). The cladogram also shows two species, *H. huillense* and *H. eylesii*, that are not supported by autapomorphies. With the exception of *H. eylesii* and *H. katakton,* which share very similar leaf anatomy and form, every other species has unique anatomical characteristics in its leaves. Although both *H. gossweilerii* and *H. huillense* have leaf blades represented only by a midvein, the blade of *H. gossweilerii* is ovoid in cross-section while there is a clear adaxial indentation (often widened into a crescent) in *H. huillense.* Neither of these states occurs in the outgroup. The other species in the genus have well developed laminas but they are inrolled in *H. conciliatus* and *H. fragile.* Both flat and inrolled laminas occur in the outgroup. *Homozeugos fragile* is unique in having conspicuously raised veins (Char. 17). Each species also appears to have a unique combination of two or more of the six types of silica bodies found in the genus but low sample sizes prevent a robust examination of this character.

Homozeugos eylesii is the most widespread and most variable species in the genus although it is internally quite consistent and easily recognizable throughout its range. I have collected it growing within a few kilometers of *H. katakton* and both species were clearly distinct. Future work likely will show an autapomorphy for the

species. It is here recognized as a metaspecies (see Donoghue 1985).

Taxonomic Treatment

Homozeugos Stapf in Hooker, Icones Plantarum. Tab. 3033.1915. TYPE SPECIES: *Homozeugos fragile* Stapf.

Caespitose perennials. Rhizomes generally short and knotty. Bud scales glabrous to sparsely pubescent, becoming shiny indurate and often stramineous. Culms unbranched, 65-189.2 cm tall; internodes glabrous to sparsely pubescent, 0.6-4.15 mm wide; nodes villous, becoming glabrous, 0.95-4.5 mm wide. Leaves with their sheath 10-59.2 cm long; lamina terete to flat, glabrous to villous, 10-72.2 cm long (excluding the most distal leaf), 0.2-6.3 mm wide, linear to lanceolate with a prominent midvein; margin minutely antorsely scabrous to entire; ligule a membrane, 0.5-48 mm long, domed to truncate, fused laterally to the auricles, entire, sometimes becoming erose. Inflorescence a panicle of 1-5 racemose segments; each segment 8.5-29.6 cm long with 18-51 spikelets; rachis segments between the spikelet pairs 2.25-14.3 mm long; pedicels 3.2-10 mm long, villous with spreading white hairs to 8.5 mm. Sessile and pedicellate spikelets identical, weakly appressed to the rachis; callus

0.8-4.2 mm long, pungent, velutinous with the hairs becoming progressively longer distally to 5 mm; first glume 5.4-11 mm long, 1.7-3.1 mm wide, the lamina symmetrical, with 2 minutely scabrous keels appearing as the margins distally, grading into the margin basally; the abaxial surface of the lamina glabrate to villous with hairs to 7 mm long; second glume 5.2-12 mm long, symmetrical, similar in texture to the first glume, glabrous to villous with hairs to 5 mm long; sterile lemma 4.8-10.2 mm long, hyaline, ovate to linear, 2-keeled, the apex acute to minutely bifid, the margins villous; fertile lemma 3.5-10 mm long, translucent, thickened in the center and apically, becoming hyaline at the margins and base, bifid at the apex, apically awned, the awn twisted basally, straight to geniculate, 14-83 mm long, glabrate to villous with hairs to 2 mm long; palea 0.5-2.5 mm long; stamens 3, the anthers 3-7.2 mm long; lodicules 0.4-0.9 mm long, cuneate. Fruit a caryopsis.

Leaves in cross-section terete to flat, with generally 3 sizes of bundles: all with an abaxial bundle cap, all but the smallest with an adaxial bundle cap; bicellular microhairs generally present on both surfaces at the edges of the costae; abaxial microhairs 36.23-61.44 µm long with their basal cell 18.83-26.33 µm long and their distal cell 16.13-38.64 µm long; adaxial microhairs 34.62-59.95 µm long

with their basal cell 17.4-29.6 µm long and their distal cell 15.87-31.29 µm long; straight trichomes to ca. 5 mm long also sometimes present. Silica bodies occurring singly in cells occurring singly or in lines.

1. Awns > 45 mm long.

    2. Ligule of penultimate leaf > 7 mm long; leaf blades flat. . . . . *H. katakton*

    2. Ligule of penultimate leaf < 7 mm long; leaf blades inrolled. . . . . *H. fragile*

1. Awns < 44 mm long.

    3. Leaf blades > 1.4 mm wide (when flattened).

        4. Ligule of penultimate leaf > 7 mm long. . . . . *H. eylesii*

        4. Ligule of penultimate leaf < 7 mm long. . . . . *H. conciliatus*

    3. Leaf blades < 1.4 mm wide.

        5. Callus > 2.5 mm long. . . . . *H. gossweileri*

        5. Callus < 2.5 mm long. . . . . *H. huillense*

1. *Homozeugos conciliatus* Guala, *sp. nov.* TYPE: Angola, Huambo, Chianga, *frequente no terreno que ladeia, á esquerda, a estrada para a Chianga,* ca. 1710m, 14 Apr. 1969, Teixeira 13216 (holotype, LISC!; isotype, LISJC!).

Affine Homozeugos eylesii sed ligulis parvum, laminas involutus et "microhairs" longioribus differt.

Eponymy. The name is a plea for peace and reconciliation in Angola. The home of this species in Huambo is the site of some of the most devastating acts aggression that have occurred amidst the the general hostilities paralyzing Angola. As a result of the war, scientific research on the countries biota has been stifled for decades.

Caespitose perennial. Rhizomes generally short and knotty. Bud scales sparsely pubescent, becoming shiny indurate and then stramineous. Culms ca. 1 m tall, 1.3-3.6 mm wide; nodes villous, 1.8-3.7 mm wide. Leaves green; sheath shorter than the lamina in the midculm leaves, 14-47.2 cm long; lamina inrolled, glabrous to sparsely hirsute, 13-59 cm long (excluding the most distal leaf), 2.3-5 mm wide (when flattened), linear to lanceolate with a prominent midvein; margin minutely antorsely scabrous; ligule 4-5.4 mm long on the penultimate leaf, 1.4-5.4 mm long overall, domed to truncate. Inflorescence of 4-5 racemose segments; each segment 8.5-14.5 cm long with 20-35 spikelets; rachis segments between the spikelet pairs 5.35-5.6 mm long; pedicels 4.3-5.2 mm long, hairs to 2.5 mm. Sessile and

pedicellate spikelets weakly appressed to the rachis; callus 1.2-1.4 mm long, pungent, velutinous, with the hairs becoming progressively longer distally, to 3 mm; first glume 7.3-8 mm long, 2.3-2.4 mm wide, the lamina with 2 minutely scabrous keels appearing as the margins, each ca. 0.6 mm wide distally grading into the margin basally; the abaxial surface of the lamina glabrate to villous with hairs to 3.6 mm long; second glume 7.3-8.1 mm long, symmetrical, similar in texture to the first glume, glabrous to villous with hairs to 1.7 mm long; sterile lemma 5.5-5.7 mm long, hyaline, ovate to linear, 2-keeled, the apex acute to minutely bifid, the margins villous; fertile lemma 6.2-7 mm long, bifid at the apex with teeth ca. 0.3 mm long, the awn straight to geniculate, 15-24 mm long, hirsute to villous with hairs to 0.5 mm long; palea 1.1-1.2 mm long; anthers 3.9-4.3 mm long, dehiscing from teardrop shaped apical pores; lodicules 0.4-0.5 mm long. Diaspore composed of the hermaphrodite spikelet with its awn. Caryopsis ca. 5 mm long (Fig. 3-4).

Leaves in cross-section flat, with generally 3 sizes of bundles: the largest and midsize bundles with bundle caps on both the adaxial and abaxial sides and spanning the thickness of the leaf, the largest with conspicuously large vessels, the midsize bundles in sets of 1-3 intercalated

between each pair of large bundles, without conspicuously large vessels, the smallest bundles intercalated in sets of 1-3, between each pair of midsize bundles, these always with an abaxial bundle cap, but without an adaxial one. Bulliform cells in discrete fan-shaped groups of ca. 5-10, in a single adaxial layer with smaller ones stacked and progressively smaller abaxially forming narrowly triangular arms between the vascular bundles, sometimes containing tannin-like substances. Both surfaces of the lamina similar in appearance with respect to the costal areas, smooth, occasionally with a few hooked prickles near the margins, the stomata in lines alternating with single or rarely pairs of fusiform cells; bicellular microhairs generally present on both surfaces at the edges of the costae; abaxial microhairs 54.24-55.14 µm long with their basal cell 22.97-23.86 µm long and their distal cell 31.26-31.28 µm long, the ratio of basal to distal cell length 0.73-0.76; adaxial microhairs 45.64-59.95 µm long with their basal cell 20.71-29.6 µm long and their distal cell 24.92-31.29 µm long, the ratio of basal to distal cell length 0.84-0.98; straight trichomes to ca. 5 mm long also sometimes present. Silica bodies occurring singly in cells that occur singly or in lines, dumbbell to 4-leaf-clover-shaped.

Phenology. The type, collected in April, is at anthesis.

Distribution and Habitat. *Homozeugos conciliatus* is known from a single locality on the road to Chianga in Huambo Province at 1710-1715 m elevation (Fig. 3-5). I estimate the coordinates to be to be ca. 12.8° S latitude and 15.75° W longitude. The habitat is characterized by the following environmental variable extrapolations from the GIS described in Chapter 4: the percentage of possible sunshine hours that are actually sunny in Jan. 36%, Feb. 40%, Mar. 38%, Apr. 49%, May 69%, Jun. 80%, Jul. 76%, Aug. 71%, Sep. 56%, Oct. 43%, Nov. 35%, Dec. 35%; mean monthly precipitation in Jan. 219 mm, Feb. 179 mm, Mar. 238 mm, Apr. 146 mm, May 14 mm, Jun. 0 mm, Jul. 0 mm, Aug. 1 mm, Sep. 20 mm, Oct. 121 mm, Nov. 228 mm, Dec. 233 mm; mean annual precipitation 1311 mm; mean monthly temperature in Jan. 19.7° C, Feb. 19.9° C, Mar. 19.9° C, Apr. 19.8° C, May 18.2° C, Jun. 16.4° C, Jul. 16.7° C, Aug. 19° C, Sep. 21° C, Oct. 20.9° C, Nov. 20° C, Dec. 19.8° C; mean annual temperature 19.2° C; surface albedo in Oct. 18%; generalized vegetation index (GVI) in Jan. 1990 134, Jul. 1990 124; percentage of

Figure 3-4. *Homozeugos conciliatus*. A. Habit. Bar equals 1 cm. B. Transverse section of a portion of the leaf lamina. Bar equals 1 mm. C. Dissection of a spikelet: left to right; first glume, second glume, sterile lemma, fertile lemma, pistil, lodicule, palea, lodicule, three anthers, callus. Bar equals 1 mm.

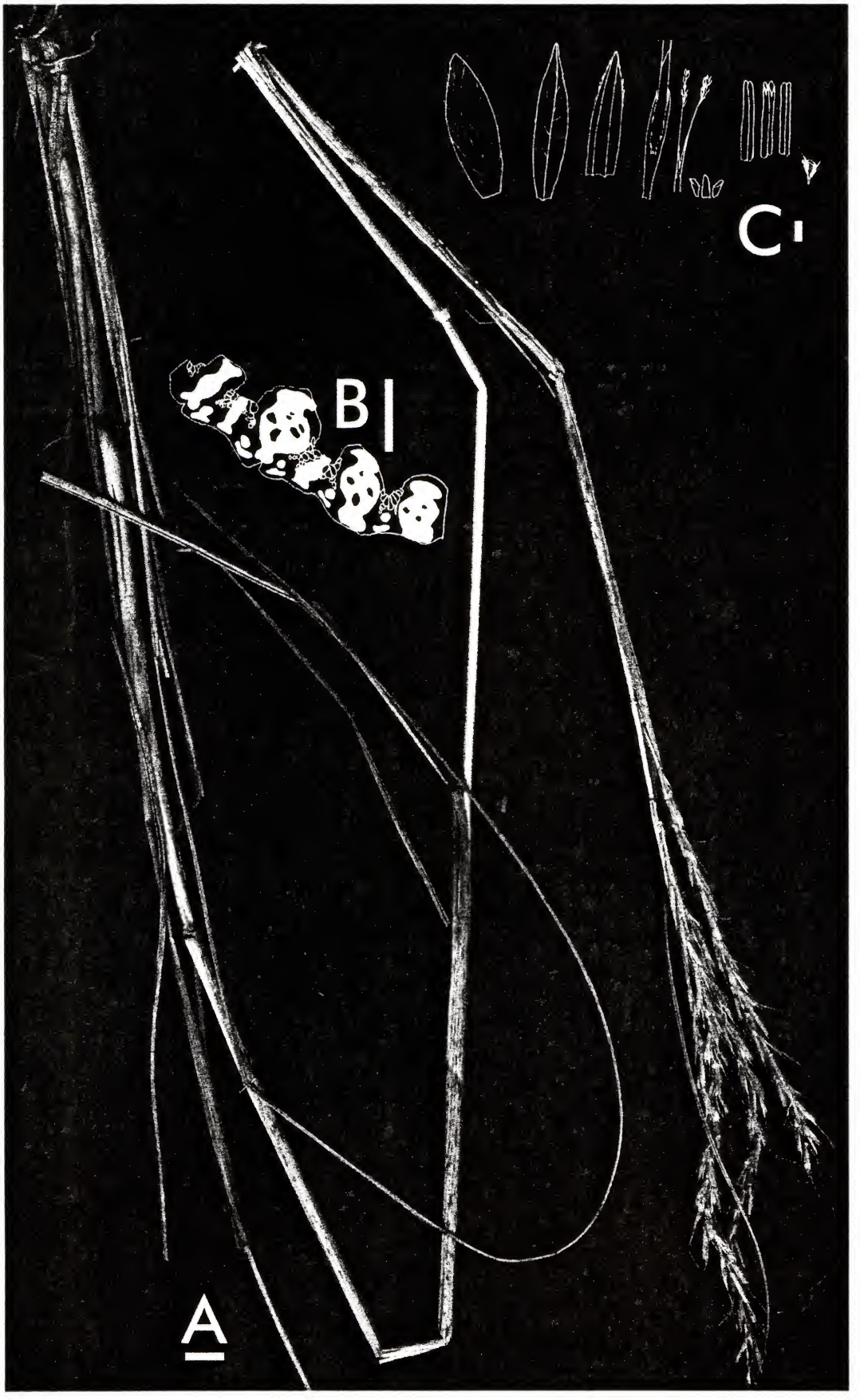

C1
B1
A

Figure 3-5. Distribution of *Homozeugos conciliatus*.

N
10°
15°
20°
15°
20°
25°
30°
35°

sand in the top 1 m of soil 51%; percentage of silt in the top 1 m of soil 17%; percentage of clay in the top 1 m of soil 32%.

2. *Homozeugos eylesii* C.E. Hubbard, Kew Bulletin 1936: 295. 1936. TYPE: Zambia, Mufulira, Eyles 8369 (holotype, K!; isotype, SRGH!).

Strongly caespitose perennial. Rhizomes always short and knotty. Bud scales sparsely pubescent, becoming shiny indurate and then stramineous. Culms medium green, quickly turning to straw colored, unbranched, 20-158 cm; internodes 0.2-2 mm wide; nodes villous to hirsute, 0.4-2.6 mm wide. Leaves bright green; sheath ca. equaling the lamina in the midculm leaves, 12.5-58 cm long; lamina glabrous to sparsely hirsute or pilose, 10-61.2 cm long (excluding the most distal leaf), 1.9-6.2 mm wide, linear to lanceolate with a prominent midvein; margin minutely antorsely scabrous; ligule hyaline to indurate membrane, 1.4-48 mm long, the ligule of the penultimate leaf 14-48 mm long, truncate. Inflorescence of 1-5 racemose segments; each segment 8.5-28.4 cm long with 18-36 spikelets; rachis segments between the spikelet pairs 5-14.25 mm long; pedicels 3.5-8 mm long, with hairs to 5.7 mm. Sessile and pedicellate spikelets moderately to weakly appressed to the

rachis; callus 0.8-1.9 mm long, with the hairs to 3.6 mm; first glume 5.7-8.9 mm long, 1.9-3 mm wide, the lamina symmetrical, with 2 minutely scabrous keels appearing as the margins, ca. 0.6 mm wide distally grading into the margin basally; the abaxial surface of the lamina glabrate to villous with hairs to 4.7 mm long; second glume 6-9 mm long, glabrous to villous with hairs to 4 mm long; sterile lemma 4.8-7.3 mm long, ovate to linear, the apex acute to minutely bifid, the margins villous; fertile lemma 5.3-7.5 mm long, bifid at the apex with teeth ca. 0.2-0.5 mm long, apically awned, the awn straight to geniculate, 14-42 mm long, glabrate to villous with hairs to 0.7 mm long; palea 0.5-2.5 mm long; anthers 3-5.2 mm long, dehiscing from teardrop shaped apical pores; lodicules 0.4-0.8 mm long. Diaspore composed of the entire spikelet with its callus, the awn and the distal 2/3 of its attached lemma deciduous upon dispersal. Caryopsis ca. 3.5-5.5 mm long (Fig. 3-6).

Leaves in cross-section flat, with generally 3 sizes of bundles: the largest and midsize bundles with bundle caps on both the adaxial and abaxial sides and spanning the thickness of the leaf, the largest with conspicuously large vessels, the midsize bundles in sets of 1-3, intercalated between each pair of large bundles, without conspicuously large vessels, the smallest bundles intercalated in sets of

1-3 between each pair of midsize bundles, these always with an abaxial bundle cap, the fibers forming the adaxial bundle cap not always contiguous along the lamina, thus some bundles appearing without a cap, spanning only the abaxial half of the leaf thickness, the other half spanned by the bulliform cells. Bulliform cells in discrete fan-shaped groups of ca. 3-9, in a single adaxial layer with smaller ones stacked and progressively smaller abaxially, forming narrowly triangular arms between the vascular bundles, often containing tannin-like substances. Both surfaces of the lamina similar in appearance with respect to the costal areas, densely papillate to smooth, the stomata in lines alternating with single or rarely pairs of fusiform cells, the fusiform cells often with a single papilla to ca. 16 µm long and 20 µm wide; bicellular microhairs generally present on both surfaces at the edges of the costae, 34.6-60 µm long with their basal cell 17.4-29.6 µm long and their distal cell 15.9-32.5 µm long, the ratio of basal to distal cell length 0.7-1.2; hooked prickles present on the costae and often grading into straight trichomes to ca. 5 mm long, the bases of the larger trichomes inflated. Silica bodies occurring singly in cells that occur singly or in lines, dumbbell to 4-leaf-clover-shaped.

Phenology. Flowering and fruiting from February to June, peaking in April.

Distribution and habitat. *Homozeugos eylesii* grows in the savannas of southern Central Africa. It is known from many types of miombo woodland including *Brachystegia* woodland, *Julbernardia* woodland, *Parinari* forest, and *Baikiakea* forest. It ranges between 8.59° and 14.61° S latitude and 24.84° and 34.05° W longitude (Fig. 3-7). The habitat is characterized by the following environmental variable extrapolations from the GIS described in Chapter 4: the percentage of possible sunshine hours that are actually sunny in Jan. 32-46%, Feb. 34-48%, Mar. 40-59%, Apr. 58-77%, May 73-86%, Jun. 75-87%, Jul. 73-91%, Aug. 79-91%, Sep. 76-88%, Oct. 68-86%, Nov. 51-71%, Dec. 34-44%; mean monthly precipitation in Jan. 182-301 mm, Feb. 169-272 mm, Mar. 121-279 mm, Apr. 27-118 mm, May 2-25 mm, Jun. 0-2 mm, Jul. 0-1 mm, Aug. 0-2 mm, Sep. 0-3 mm, Oct. 5-33 mm, Nov. 45-181 mm, Dec. 163-277 mm; mean annual precipitation 960-1448 mm; mean monthly temperature in Jan. 17.8-23.5° C, Feb. 18.1-23.3° C, Mar. 18.2-23.2° C, Apr. 18.3-23.3° C, May 16.8-22.3° C, Jun. 14.8-20.9° C, Jul. 14.5-20.7° C, Aug. 15.9-22.1° C, Sep. 17.9-24° C, Oct. 20.1-25.5° C, Nov. 19.5-25° C, Dec. 18.2-23.9° C; mean annual temperature 19.9-22.3° C; surface albedo in Oct. 0-18%; generalized vegetation index (GVI) in

Jan. 1990 122-156, Jul. 1990 123-139; percentage of sand in the top 1 m of soil 0-94%; percentage of silt in the top 1 m of soil 0-23%; percentage of clay in the top 1 m of soil 0-59%. The following environmental measurements were taken directly from soil samples taken with every Guala collection (listed below): pH in 0.1M $CaCl_2$ 3.7-5.1; exchangeable Ca 0-1.6 Me/100g; exchangeable Mg 0-0.8 Me/100g; exchangeable Na 0.02-0.07 Me/100g; exchangeable K 0.02-0.45 Me/100g; total exchangeable bases (TEB) 0.3-2.5 Me/100g; cation exchange capacity (CEC) 1.5-4.5 Me/100g; base saturation 10-73%; CEC/100g of Clay (E/C) 8.7-128.2; TEB/100g of clay (S/C) 0.8-75.7; exchangeable sodium percentage (ESP) 0.7-4%; exchangeable potassium percentage (EKP) 0.7-10%; fine sand 12-54%; medium sand 15-64%; coarse sand 3-36%; Silt 2-66%; Clay 2-41%; hue of soil wet 2.5-10YR, dry 2.5-10YR; color value of soil wet 2-5, dry 4-7; chroma of soil wet 1-6, dry 1-6; bulk density 0.65-1.35 g/cm^3.

Additional specimens examined. DEMOCRATIC REPUBLIC OF CONGO. Shaba: Kasumbeleza, 9 Apr. 1995, Guala 1737 (BR, FLAS, MRSC, PRE, US); Kasumbeleza, 20 Mar. 1971, Lisouski 552 (BR), 555 (BR).

MALAWI. Northern Province: Near Choma, 26 Apr. 1995, Guala 1764 (FLAS, MAL, PRE, US); Near Mzuzu, 26 Apr. 1995, Guala 1765 (FLAS, MAL, PRE, US); Mtangatanga Forest Reserve,

20 May 1951, Jackson 431 (PRE); Nkhata Bay District, 2 Jun. 1974, Pawek 8674 (BR, MO, SRGH, UC).

TANZANIA. Rukwa: Mt. Chesa, 23 Apr. 1995, Guala 1757 (DSM, FLAS, PRE, US); Mt. Mumbo, 23 Apr. 1995, Guala 1758 (DSM, FLAS, PRE, US); Kasanga - Forest Reserve, 31 Mar. 1959, Webster T237 (SRGH).

ZAMBIA. Central Province: Near Ndabala, 10 Apr. 1995, Guala 1742 (FLAS, MRSC, PRE, US); Serenje, 10 Apr. 1995, Guala 1743 (FLAS, MRSC, PRE, US); 40 km N of Serenje, 11 Apr. 1995, Guala 1744 (FLAS, MRSC, PRE, US); 65.6 km N of Serenje, 11 Apr. 1995, Guala 1748 (FLAS, MRSC, PRE, US); Serenje, 5 Apr. 1961, Phipps 2957 (SRGH). Copperbelt: Mufulira, 9 May 1934, Eyles 8371 (PRE, SRGH); Mufulira, 8 April 1995, Guala 1729 (FLAS, MRSC, PRE, US); Kitwe, 9 Apr. 1995, Guala 1730 (FLAS, MRSC, PRE, US); between Chingola and Chililabombwe, 9 Apr. 1995, Guala 1734 (FLAS, MRSC, PRE, US); near Chililabombwe, 9 Apr. 1995, Guala 1736 (FLAS, MRSC, PRE, US); near Kasumbeleza, 9 Apr. 1995, Guala 1738 (FLAS, MRSC, PRE, US) Kasumbeleza, 9 Apr. 1995, Guala 1739 (FLAS, MRSC, PRE, US); Kitwe, 25 Mar. 1966, Mutimushi 1333 (SRGH); Ndola, 4 May 1959, Vesey-Fitzgerald 2568 (SRGH). Lusaka Province: Luano, 17 Mar. 1966, Fanshawe 9637 (SRGH). Northern Province: Mpika, 29 Mar. 1961, Angus 2569 (SRGH); Luwingu, 13 May 1964, Astle 3012 (SRGH); 6.5 km N of Salamo,

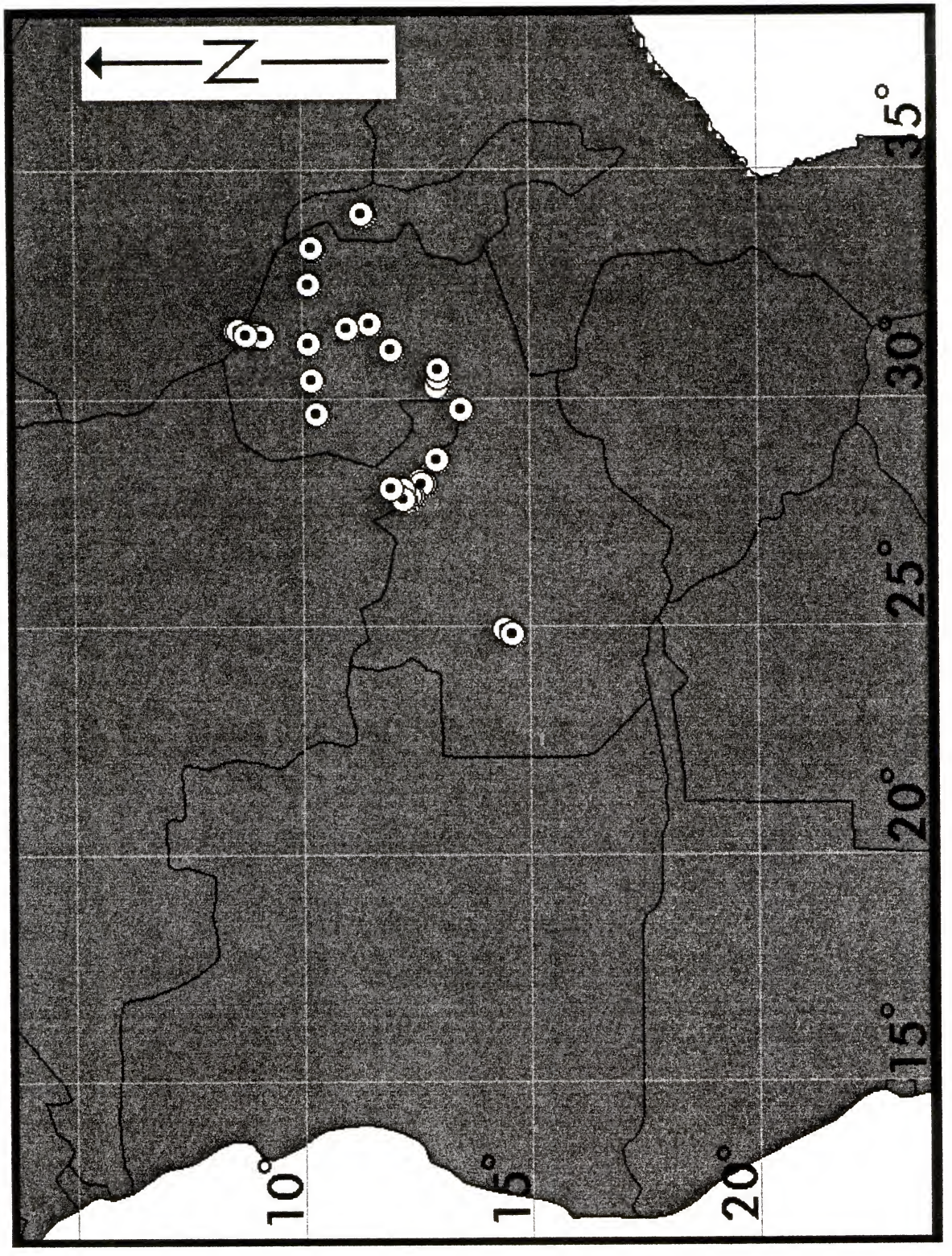
11 Apr. 1995, Guala 1751 (FLAS, MRSC, PRE, US); near Mpika, 12 Apr. 1995, Guala 1752 (FLAS, MRSC, PRE, US); 55 km E of Luwingo, 12 Apr. 1995, Guala 1753 (FLAS, MRSC, PRE, US); Kasama, 22 Apr. 1995, Guala 1754 (FLAS, MRSC, PRE, US); 38.6K S of Mbala, 22 Apr. 1995, Guala 1755 (FLAS, MRSC, PRE, US); between Mosi and Mbala, 23 Apr. 1995, Guala 1756 (FLAS, MRSC, PRE, US); N of Mpika, 24 Apr. 1995, Guala 1759 (FLAS, MRSC, PRE, US); S of Isoka, 24 Apr. 1995, Guala 1760 (FLAS, MRSC, PRE, US); 34 km N of Muyombe, 26 Apr. 1995, Guala 1762 (FLAS, MRSC, PRE, US); 23 km N of Muyombe, 26 Apr. 1995, Guala 1763 (FLAS, MRSC, PRE, US); Chinakila, near Mbala, 11 Apr. 1956, Vesey-Fitzgerald 1033 (SRGH); Chila, near Mbala, 10 Apr. 1958, Vesey-Fitzgerald 1608 (SRGH); Ndundu, 3 Apr. 1959, Webster A264 (SRGH). Western Province: 59 km from Kaoma on the Kesempe Rd., 12 July 1994, Guala 1666 (FLAS, MRSC, PRE, US); 34 km from Kaoma on the Kesempe Rd., 12 July 1994, Guala 1667 (FLAS, MRSC, PRE, US).

3. *Homozeugos fragile* Stapf in Hooker, Icones Plantarum. Tab. 3033. 1915. TYPE: Angola, Benguella; the country of the Ganguellas and Ambuellas, received 1910, Gossweiler 4029 (holotype, K!; isotype, US!). This collection is almost certainly not from the current coastal city of Benguela (spelled with only one "L") as

Figure 3-6. *Homozeugos eylesii*. A. Inflorescence. Bar equals 1 cm. B. Transverse section of a portion of a leaf lamina. Bar equals 1 mm. C. Habit. Bar equals 10 cm. D. Dissection of a spikelet: left to right; first glume second glume, sterile lemma, fertile lemma, pistil, lodicule, palea, lodicule, three anthers, callus. Bar equals 1 mm.

A
B
C
D

Figure 3-7. Distribution of *Homozeugos eylesii*.


N
10°
15°
20°
15°
20°
25°
30°
35°

interpreted by Clayton (1973) but from Central Angola where the Ambuellas and Ganguellas were based and, most likely, near the locality written on several other labels of this set (apparently by the collector) at LISCJ, i.e., Bie, Cuito, Margem do rio Tiengo, Menongue. The current city of Cuito (formerly Silva Porto), in the province of Bie, is in the homeland of the Ganguellas. Gossweiler's collection numbers 2586 and 3774 were made there in March of 1906; this collection appears to be from the same set and it is likely that it was collected then and there as well.

Caespitose perennial. Rhizomes generally short and knotty. Bud scales villous, becoming stramineous. Culms unbranched, ca. 1 m tall; internodes 1.6-2.9 mm wide; nodes villous, 1.6-3.2 mm wide. Leaves villous; sheath shorter than the lamina in the midculm leaves, 18-33 cm long; lamina inrolled, villous on both surfaces, 30-48.5 cm long (excluding the most distal leaf), 1.6-4 mm wide (when flattened), lanceolate when flattened with a prominent midvein; margin minutely antorsely scabrous; ligule 2.3-3.2 mm long, the ligule of the penultimate leaf 2.6-3.2 mm long, domed to truncate. Inflorescence of ca. 1-4 racemose segments; each segment ca. 14-16.5 cm long; rachis segments between the spikelet pairs 9-11 mm long; pedicels 4.5-6 mm

long, with hairs to 4.7 mm. Sessile and pedicellate spikelets weakly appressed to the rachis; callus 4-4.2 mm long, pungent, with hairs to 4.2 mm; first glume 9.3-10.4 mm long, 2.2-2.5 mm wide, the abaxial surface of the lamina with hairs to 7 mm long; second glume 9.6-10.1 mm long, with hairs to 4.7 mm long; sterile lemma 7.5-8 mm long, ovate to linear, the apex acute to minutely bifid, the margins villous; fertile lemma 7.3-7.5 mm long, bifid at the apex with teeth ca. 0.5 mm long, the awn, straight to geniculate, 65-83 mm long, hirsute to villous with hairs to 2 mm long; palea 1.5-1.6 mm long; anthers 5.7-6.4 mm long; lodicules 0.6-0.8 mm long, cuneate. Diaspore of the entire hermaphrodite spikelet but often excluding the awn and its attached lemma which are quickly deciduous. Fruit a caryopsis (mature fruit not seen) (Fig. 3-8).

Leaves in cross-section laminar and inrolled, with generally 3 sizes of bundles: the largest and midsize bundles with bundle caps on both the adaxial and abaxial sides and spanning the thickness of the leaf, the largest with conspicuously large vessels, the midsize bundles intercalated between each pair of small bundles, without conspicuously large vessels, the smallest bundles intercalated between each pair of midsize bundles (or a midsize and a large bundle), these always with an abaxial

bundle cap, but without an adaxial one. Bulliform cells in discrete fan-shaped groups of ca. 5-10, in a single adaxial layer, sometimes containing tannin-like substances. The costal areas of both surfaces of the lamina similar in appearance, smooth except for hooked prickles, which are common but obscured by and grading into ubiquitous trichomes to 5 mm, the stomata in lines alternating with single or rarely pairs of fusiform cells; bicellular microhairs generally present on both surfaces at the edges of the costae; abaxial microhairs not measured; adaxial microhairs 43.5-49.73 µm long with their basal cell 23.32-25.25 µm long and their distal cell 20.19-24.48 µm long, the ratio of basal to distal cell length 1.03-1.16. Silica bodies occurring singly in cells that occur singly or in lines, two-lobed, longitudinally oriented.

Phenology. The holotype is at pre-anthesis while the isotype is at anthesis. As explained above, it is likely that the collection was made in March or later.

Distribution and habitat. *Homozeugos fragile* is known from a single locality, probably near the present city of Cuito, which is at ca. 12.38° S latitude and 16.95° W longitude and surrounded by generally dry savanna and grassland at ca. 1700 m (Fig. 3-9). The habitat is characterized by the following environmental variable

Figure 3-8. *Homozeugos fragile*. A. Spikelet dissection: top to bottom; three anthers, sterile lemma, second glume, first glume, fertile lemma, lodicule, palea, lodicule, callus. Bar equals 1 mm. B. Partial inflorescence. Bar equals 1 cm. C. Habit. Bar equals 10 cm. D. Transverse section of a portion of the leaf lamina. Bar equals 1 mm.

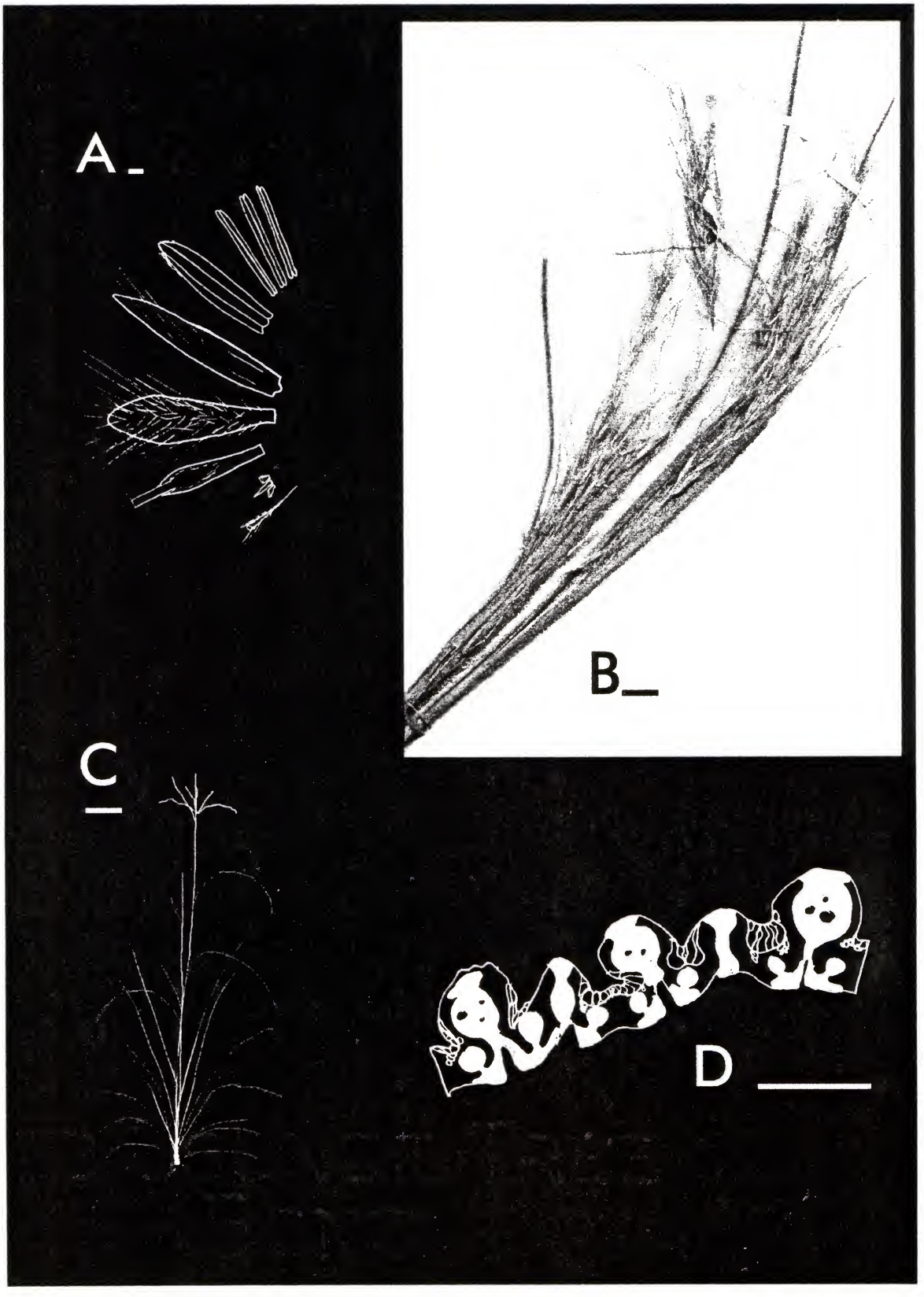

A
B
C
D

Figure 3-9. Distribution of *Homozeugos fragile*.

N
35°
30°
25°
20°
15°
10°
15°
20°

extrapolations from the GIS described in Chapter 4: the percentage of possible sunshine hours that are actually sunny in Jan. 34%, Feb. 39%, Mar. 37%, Apr. 49%, May 69%, Jun. 80%, Jul. 77%, Aug. 71%, Sep. 56%, Oct. 44%, Nov. 35%, Dec. 33%; mean monthly precipitation in Jan. 197 mm, Feb. 195 mm, Mar. 207 mm, Apr. 85 mm, May 10 mm, Jun. 0 mm, Jul. 0 mm, Aug. 4 mm, Sep. 22 mm, Oct. 107 mm, Nov. 195 mm, Dec. 213 mm; mean annual precipitation 1290 mm; mean monthly temperature in Jan. 19° C, Feb. 19.1° C, Mar. 19.1° C, Apr. 19.1° C, May 17.1° C, Jun. 15.1° C, Jul. 15.1° C, Aug. 17.1° C, Sep. 20° C, Oct. 20° C, Nov. 19.1° C, Dec. 19° C; mean annual temperature 19.2° C; surface albedo in Oct. 18%; generalized vegetation index (GVI) in Jan. 1990 129, Jul. 1990 116; percentage of silt in the top 1 m of soil 17%; percentage of clay in the top 1 m of soil 32%.

4. *Homozeugos gossweileri* Stapf in Prain, Flora of Tropical Africa 9: 103. 1917. TYPE: Angola, Bie, Cuito, Margem do rio Tiengo, Menongue; [not Benguela *fide* Clayton (1973)]. Gossweiler 2586 (holotype, K!; isotype, LISCJ!).

Strongly caespitose perennial. Rhizomes generally short and knotty. Bud scales becoming stramineous. Culms unbranched, 70-103 cm; internodes 1.65-2.9 mm wide; nodes

villous becoming glabrate, 1.6-1.75 mm wide. Leaves with their sheath shorter than the lamina, 11-24 cm long; lamina pilose, terete to ovate in cross-section, 44.5-66.3 cm long (excluding the most distal leaf), 0.2-1 mm wide, linear; margin entire; ligule 0.5-1.4 mm long, the ligule of the penultimate leaf ca. 1.4 mm long, truncate. Inflorescence of 1-2 racemose segments; each segment 10.4-17.9 cm long with 26-36 spikelets; rachis segments between the spikelet pairs 5.6-8.6 mm long; pedicels 5-5.6 mm long, with hairs to 5 mm. Sessile and pedicellate spikelets weakly appressed to the rachis; callus 2.8-3 mm long, pungent, velutinous with the hairs to 2.4 mm; first glume 8.3-9 mm long, 2-2.2 mm wide, with 2 minutely scabrous keels appearing as the margins distally, grading into the true margin basally; the abaxial surface of the lamina villous with hairs to 3 mm long; second glume 9-9.4 mm long, villous with hairs to 1.6 mm long; sterile lemma 7.3-7.4 mm long, obovate to linear, the apex acute to rounded, the margins villous; fertile lemma 7-7.7 mm long, bifid at the apex with teeth ca. 0.3 mm long, the awn weakly geniculate, 32-36 mm long, villous with hairs to 0.6 mm long; palea 0.7-0.8 mm long; anthers 4.2-4.3 mm long; lodicules 0.6-0.7 mm long. Diaspore composed of the entire spikelet with its callus, the awn and the distal

2/3 of its attached lemma deciduous upon dispersal. Mature fruit not seen (Fig. 3-10).

Leaves in cross-section terete to ovate, essentially reduced to the midvein, the adaxial surface limited to ca. 1/8 the diameter of the leaf, the other 7/8 with vascular bundles characteristic of the abaxial surface in other species; larger bundles with bundle caps on both ends, the smallest with only an abaxial cap; bulliform cells lacking; adaxial surface of the lamina with a few minute papillae grading into hooked prickles; stomata lacking; abaxial surface of ca. 5-14 lines of stomata and their associated fusoid cells alternating with a similar width group of lines of fusoid cell/silica cell pairs, the silica bodies ranging from dumbbell or 4-leaf clover shaped with the long axis longitudinal to ovoid with the long axis lateral; bicellular microhairs generally present on both surfaces, 36.04-43.59 µm long with their basal cell 18.74-22.83 µm long and their distal cell 17.31-20.76 µm long, the ratio of basal to distal cell length 1.08-1.1; prickles not present; trichomes to ca. 5 mm long common, their bases inflated.

Phenology. The only collection was made in March; the flowers of the type specimen are mostly at, or just beyond dehiscence.

Figure 3-10. *Homozeugos gossweileri*. A. Habit. Bar equals 1 cm. B. Dissection of a spikelet: from the bottom up; first glume, callus, second glume, sterile lemma, fertile lemma, lodicule, palea, lodicule, three anthers. Bar equals 1 mm. C. Transverse section of a portion of the leaf lamina. Bar equals 1 mm.

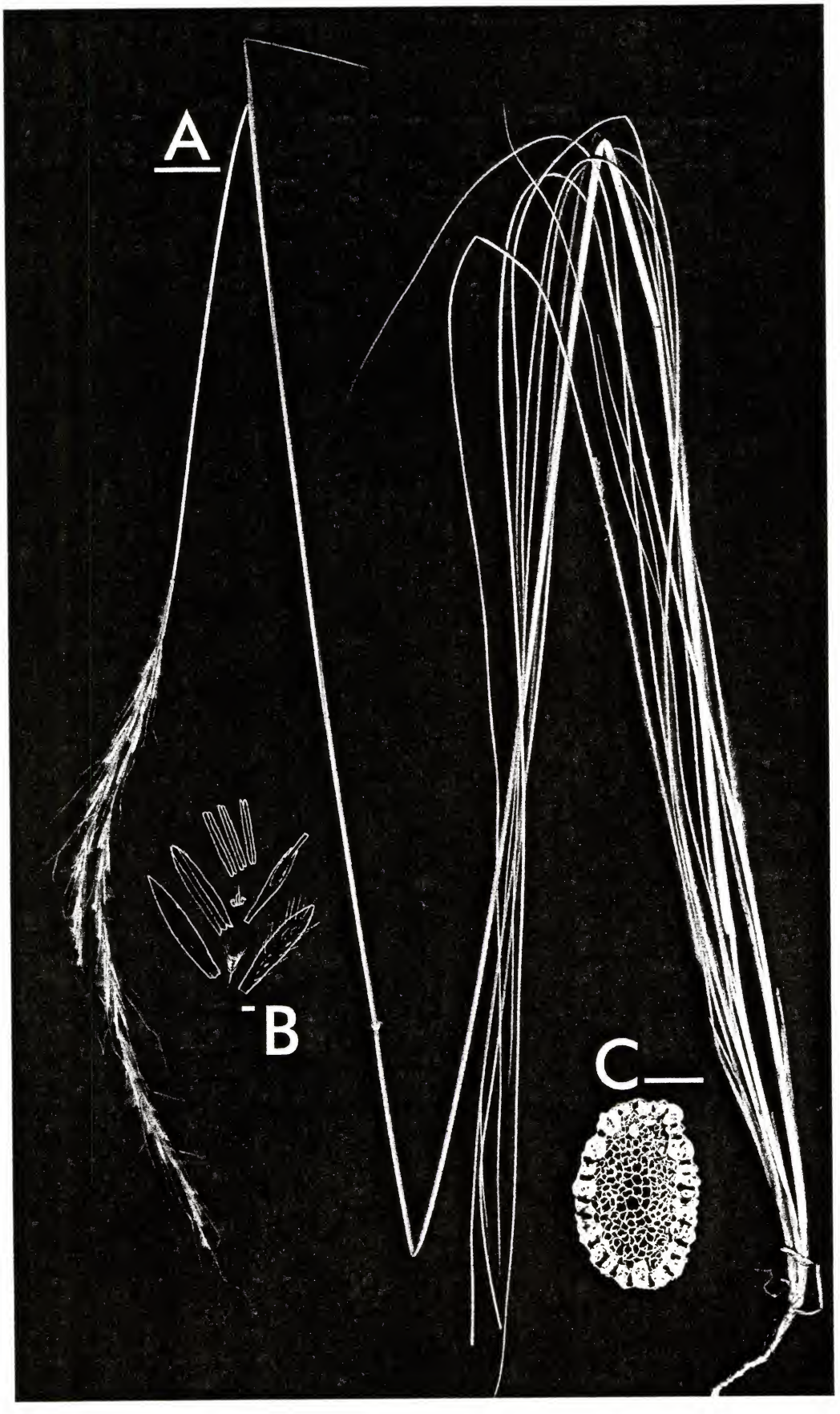

A
B
C

Figure 3-11. Distribution of *Homozeugos gossweileri*.

N
10°
15°
20°
15°
20°
25°
30°
35°

Distribution and habitat. The label of the type of *Homozeugos gossweileri* indicates that it was collected in dry scrubby vegetation along a river. The locality appears to be at ca. 12.83° S latitude and 16.95° W longitude (Fig. 3-11). The habitat is characterized by the following environmental variable extrapolations from the GIS described in Chapter 4: the percentage of possible sunshine hours that are actually sunny in Jan. 34%, Feb. 39%, Mar. 37%, Apr. 49%, May 69%, Jun. 80%, Jul. 77%, Aug. 71%, Sep. 56%, Oct. 44%, Nov. 35%, Dec. 33%; mean monthly precipitation in Jan. 197 mm, Feb. 195 mm, Mar. 207 mm, Apr. 85 mm, May 10 mm, Jun. 0 mm, Jul. 0 mm, Aug. 4 mm, Sep. 22 mm, Oct. 107 mm, Nov. 195 mm, Dec. 213 mm; mean annual precipitation 1290 mm; mean monthly temperature in Jan. 19° C, Feb. 19.1° C, Mar. 19.1° C, Apr. 19.1° C, May 17.1° C, Jun. 15.1° C, Jul. 15.1° C, Aug. 17.1° C, Sep. 20° C, Oct. 20° C, Nov. 19.1° C, Dec. 19° C; mean annual temperature 19.2° C; surface albedo in Oct. 18%; generalized vegetation index (GVI) in Jan. 1990 129, Jul. 1990 116; percentage of sand in the top 1 m of soil 51%; percentage of silt in the top 1 m of soil 17%; percentage of clay in the top 1 m of soil 32%.

5. *Homozeugos huillense* (Rendle) Stapf in Hooker, Icones Plantarum tab. 3033. 1915. *Pollinia huillensis* Rendle,

Catalogue of the African Plants collected by Friderich Welwitsche in 1853-61 2: 136. 1899. *Pogonatherum huillense* (Rendle) Roberty, Boissiera 9: 381. 1960. TYPE: Angola, Huilla, near Empalanca, Welwitsch 2669 (holotype, BM; isotype K!).

Strongly caespitose perennial. Rhizomes short and knotty. Bud scales glabrous to glabrate, becoming stramineous. Culms, 80-118 cm; internodes, 1-2.8 mm wide; nodes villous to hirsute, becoming glabrous with age, 1.5-3.4 mm wide. Leaf sheath shorter than the lamina in the midculm leaves, 12.5-58 cm long; lamina pilose, becoming glabrate except at the base, 11-57 cm long (excluding the most distal leaf), 0.4-1.15 mm wide, linear; margin minutely antorsely scabrous; ligule hyaline, 1-6 mm long, the ligule of the penultimate leaf 2-6 mm long, truncate, entire. Inflorescence of 1-5 racemose segments; each segment 8.9-18.9 cm long with 20-49 spikelets; rachis segments between the spikelet pairs 2.25-6.8 mm long; pedicels 3.2-4.5 mm long, with hairs to 6 mm. Sessile and pedicellate spikelets moderately to weakly appressed to the rachis; callus 1.3-2.3 mm long, with hairs to 5 mm; first glume 5.4-8 mm long, 1.8-2.5 mm wide, with 2 minutely scabrous keels appearing as the margins, ca. 0.5 mm wide distally grading into the margin basally; the abaxial surface of the lamina villous with

hairs to 3.8 mm long; second glume 5.2-7.6 mm long, villous with hairs to 3.8 mm long; sterile lemma 5-7 mm long, ovate to linear, 2-keeled, the apex acute to minutely bifid, the margins villous; fertile lemma 3.5-6.5 mm long, bifid at the apex with teeth ca. 0.2-0.4 mm long, the awn weakly geniculate, 24-40 mm long, glabrate to villous with hairs to 0.9 mm long; palea 0.7-1.9 mm long; anthers 3.4-4.3 mm long, dehiscing from teardrop shaped apical pores; lodicules 0.5-0.7 mm long. Diaspore composed of the entire spikelet with its callus, the awn and the distal 2/3 of its attached lemma deciduous upon dispersal. Fruit a caryopsis (Fig. 3-12).

Leaves in cross-section crescent shaped, the adaxial surface slightly more than half the size of the abaxial surface at midleaf, essentially an expanded midvein without lateral lamina; vascular bundles of 3 sizes; larger bundles with bundle caps on both ends, the smallest with only an abaxial cap; bulliform cells lacking; adaxial surface densely covered with hooked prickles, some grading into trichomes to ca. 5 mm long; stomata lacking; bicelluar microhairs rarely present near the margins, ca. 39.06 µm long with their basal cell ca. 20.66 µm long and their distal cell ca. 18.4 µm long, the ratio of basal to distal cell length ca. 1.23; abaxial surface with widely scattered lines of hooked prickles on costal ridges, lines of stomata

and fusiod cells making up the intercostal regions with parallel lines of fusoid cells mostly containing silica bodies over the vascular bundles; silica bodies dumbbell shaped to 4-leaf-clover-shaped; bicellular microhairs generally present at the edges of the costae, 36.23-47.55 µm long with their basal cell 19.81-24.06 µm long and their distal cell 16.13-24.06 µm long, the ratio of basal to distal cell length 0.98-1.26.

Phenology. Flowering peaking in April and May.

Distribution and habitat. *Homozeugos huillense* grows in the savannas and forest edges of central Angola. It ranges from 15-17° S latitude, 13.37-14.03° W longitude and from 900-2000 m elevation (3-13). The habitat is characterized by the following environmental variable extrapolations from the GIS described in Chapter 4: the percentage of possible sunshine hours that are actually sunny in Jan. 49-57%, Feb. 50-57%, Mar. 49-57%, Apr. 57-64%, May 72-73%, Jun. 72-76%, Jul. 64-70%, Aug. 56-63%, Sep. 49-52%, Oct. 48-52%, Nov. 46-53%, Dec. 47-54%; mean monthly precipitation in Jan. 58-162 mm, Feb. 75-183 mm, Mar. 52-216 mm, Apr. 20-106 mm, May 0-8 mm, Jun. 0 mm, Jul. 0 mm, Aug. 0-1 mm, Sep. 0-11 mm, Oct. 5-85 mm, Nov. 19-150 mm, Dec. 43-164 mm; mean annual precipitation 614-892 mm; mean monthly temperature in Jan. 19.7-22.3° C, Feb. 19.4-22.2° C, Mar.

20.4-22.5° C, Apr. 18.8-22.1° C, May 15.4-20.4° C, Jun. 8.1-18.8° C, Jul. 11.8-19.3° C, Aug. 13.3-21.5° C, Sep. 16-23.8° C, Oct. 17.8-23.9° C, Nov. 19.3-23.2° C, Dec. 19.4-22.5° C; mean annual temperature 19.5-22.1° C; surface albedo in Oct. 15.6-18%; generalized vegetation index (GVI) in Jan. 1990 117-125, Jul. 1990 109-121; percentage of sand in the top 1 m of soil 51-80%; percentage of silt in the top 1 m of soil 15-18%; percentage of clay in the top 1 m of soil 5-32%.

Additional specimens examined. ANGOLA. Huila: Capelougo, 20 May 1959, Fereira 772 (LISC); Humpata, 5 Jun. 1937, Gossweiler 10726 (US); Ruacana, 9 May 1937, Gossweiler 11116 (US); Mahungo, 10 Apr. 1958, Teixeira 3381 (LISC); Humpata, 10 Apr. 1958, Teixeira 3444 (LISC, PRE).

6. *Homozeugos katakton* Clayton, Garcia de Orta 1: 11-12. 1973. TYPE: Angola, Bie, Moxico [sic], Munhango Gossweiler 11260 (holotype, K!; isotype US!).

Strongly caespitose perennial. Rhizomes distinctly short and knotty. Bud scales sparsely pubescent, becoming shiny indurate. Culms 123.3-189.2 cm; internodes 1.2-4.15 mm wide; nodes villous to hirsute, 2.1-4.5 mm wide, those of the lower nodes 3.9-4.5 mm wide. Leaf sheath equaling or shorter than the lamina in the midculm leaves, 19.5-59.2 cm long; lamina sparsely hirsute to pilose, 35-72.2 cm long

Figure 3-12. Illustration of *Homozeugos huillense*. A. Habit. Bar equals 1 cm. B. Transverse section of a portion of the leaf lamina. Bar equals 1 mm. C. Dissection of a spikelet: from top to bottom and left to right; first glume, second glume, callus, fertile lemma, sterile lemma, lodicule, palea, lodicule, three anthers. Bar equals 1 mm.

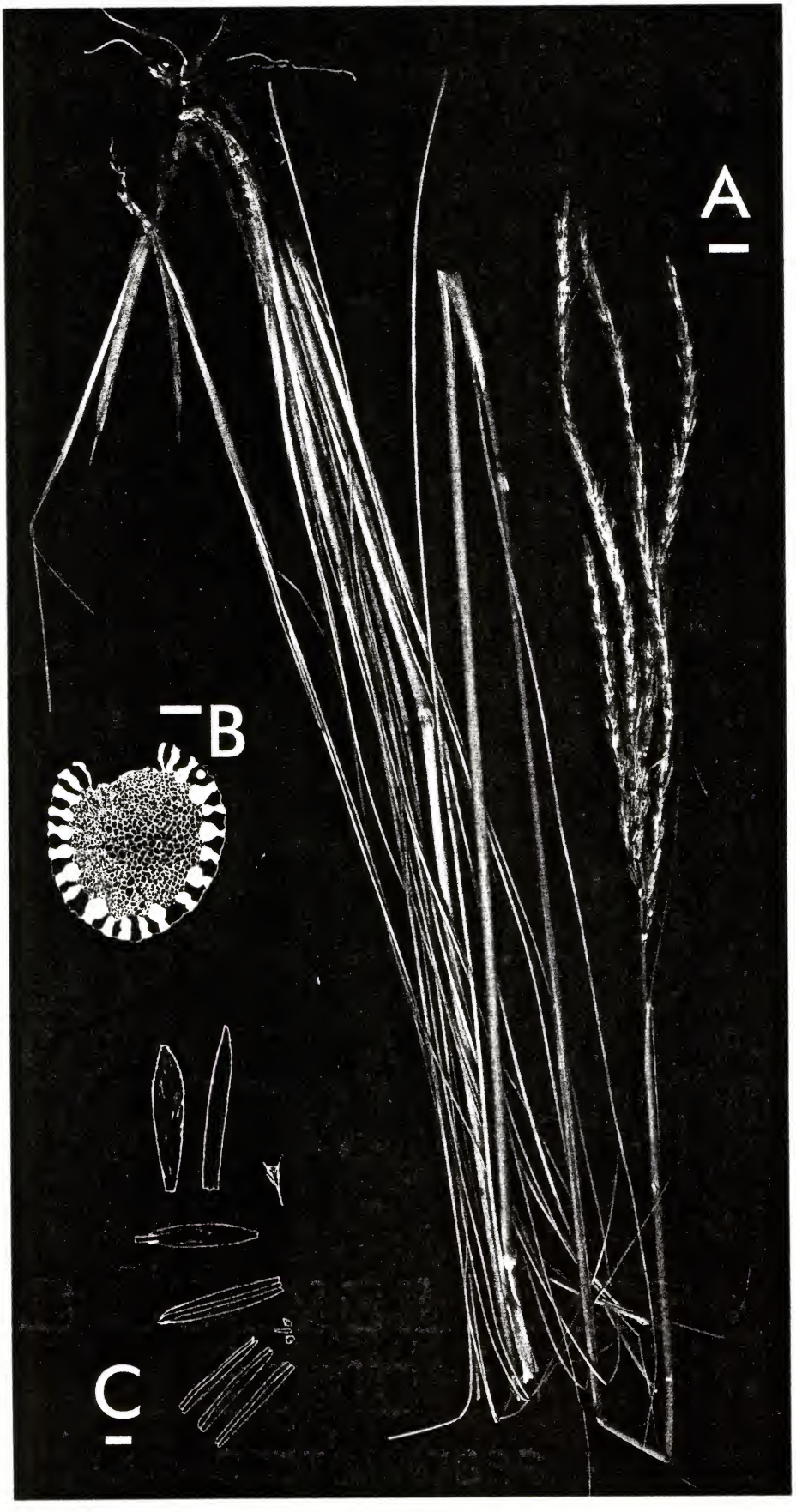

A
B
C

Figure 3-13. Distribution of *Homozeugos huillense*.

N
10°
15°
20°
15°
20°
25°
30°
35°

(excluding the most distal leaf), 2.8-6.3 mm wide, linear to lanceolate with a prominent midvein; margin minutely antorsely scabrous; ligule hyaline to indurate, 2-32.5 mm long, the ligule of the penultimate leaf 12-32.5 mm long, truncate to erose. Inflorescence of 2-5 racemose segments; each segment 13.5-29.6 cm long with 22-51 spikelets; rachis segments between the spikelet pairs 9.1-14.3 mm long; pedicels 5.3-10 mm long, with hairs to 8.5 mm. Sessile and pedicellate spikelets weakly to strongly appressed to the rachis; callus 3.2-4.1 mm long, pungent, with hairs to 4 mm; first glume 9.3-11 mm long, 2.5-3.1 mm wide, the lamina with 2 minutely scabrous keels appearing as the margins, ca. 0.6-0.7 mm wide distally, grading into the margin basally; the abaxial surface of the lamina hirsute with hairs to 6 mm long; second glume 9.8-12 mm long, sparsely hirsute to villous with hairs to 5 mm long; sterile lemma 8.5-10.2 mm long, ovate to linear, the apex acute to minutely bifid, the margins villous; fertile lemma 8-10 mm long, bifid at the apex with teeth ca. 0.4-0.5 mm long, the awn geniculate, 45-76 mm long, villous with hairs to 1.2 mm long; palea 1.2-1.6 mm long; anthers 5.5-7.2 mm long, dehiscing from teardrop shaped apical pores; lodicules 0.6-0.9 mm long. Diaspore composed of the entire spikelet with its callus, the awn and

the distal 2/3 of its attached lemma deciduous upon dispersal. Caryopsis ca. 10 mm long (Fig. 3-14).

Leaves in cross-section flat, with generally 3 sizes of bundles: the largest and midsize bundles with bundle caps on both the adaxial and abaxial sides and spanning the thickness of the leaf, the largest with conspicuously large vessels, the midsize bundles in sets of 1-4, intercalated between each pair of large bundles, without conspicuously large vessels, the smallest bundles intercalated in sets of 1-3 between each pair of midsize bundles or between a midsize and a large, these always with an abaxial bundle cap, the fibers forming the adaxial bundle cap not always contiguous along the lamina, thus some bundles rarely appearing without a cap, spanning only the abaxial half of the leaf thickness, the other half spanned by the bulliform cells. Bulliform cells in discrete fan-shaped groups of ca. 3-10, in a single adaxial layer with smaller ones stacked and progressively smaller abaxially forming narrowly triangular arms between the vascular bundles, often containing tannin-like substances. Both surfaces of the lamina similar in appearance with respect to the costal areas, densely covered with papillae and hooked prickles, the stomata in lines alternating with single or rarely pairs of fusiform cells, the fusiform cells often with a single

papilla, to ca. 15 µm long and 22 µm wide, or a hooked spine, these sometimes grading into trichomes; bicellular microhairs generally present on both surfaces at the edges of the costae; adaxial microhairs 53.28-53.68 µm long with their basal cell 21.74-25.75 µm long and their distal cell 27.92-31.54 µm long, the ratio of basal to distal cell length 0.69-0.92; abaxial microhairs 61.44-64.97 µm long with their basal cell 25.44-26.33 µm long and their distal cell 36-38.64 µm long, the ratio of basal to distal cell length 0.68-0.71; hooked prickles present on the costae and often grading into straight trichomes to ca. 5 mm long, the bases of the larger trichomes inflated. Silica bodies occurring singly in cells that occur singly or in lines, dumbbell to 4-leaf-clover-shaped.

Phenology. Gossweiler's collections were all made in May and show a range from pre-dehiscence to post-dehiscence. My own collection was made in June when the plants were long past flowering and dispersing fruit.

Distribution and habitat. *Homozeugos katakton* grows in the savannas of eastern Anogla and western Zambia. It is known from various shrublands in Angola and was collected in a dry woodland dominated by *Burkea africana* and *Erythrophleum africanum* in western Zambia. The species is known from 12.3-15.19° S latitude and 18.25-24.53° W

longitude (Fig. 3-15). The habitat is characterized by the following environmental variable extrapolations from the GIS described in Chapter 4: the percentage of possible sunshine hours that are actually sunny in Jan. 33-42%, Feb. 38-44%, Mar. 38-55%, Apr. 52-77%, May 72-86%, Jun. 82-87%, Jul. 79-88%, Aug. 74-87%, Sep. 59-80%, Oct. 47-70%, Nov. 36-54%, Dec. 33-44%; mean monthly precipitation in Jan. 215-252 mm, Feb. 172-224 mm, Mar. 121-228 mm, Apr. 27-95 mm, May 1-11 mm, Jun. 0-1 mm, Jul. 0 mm, Aug. 0-4 mm, Sep. 2-19 mm, Oct. 28-105 mm, Nov. 102-192 mm, Dec. 223-228 mm; mean annual precipitation 944-1386 mm; mean monthly temperature in Jan. 21.3-23.3° C, Feb. 21.3-23.4° C, Mar. 22.4-23.4° C, Apr. 21.2-23° C, May 1-11° C, Jun. 15.1-17.6° C, Jul. 14.9-17.9° C, Aug. 17.7-20.6° C, Sep. 21.1-24.5° C, Oct. 22.2-26° C, Nov. 21.2-24.3° C, Dec. 21.2-23.5° C; mean annual temperature 19.9-22.1° C; surface albedo in Oct. 18%; generalized vegetation index (GVI) in Jan. 1990 130-142, Jul. 1990 125-135; percentage of sand in the top 1 m of soil 87-95%; percentage of silt in the top 1 m of soil 0-2%; percentage of clay in the top 1 m of soil 3-12%. The following environmental measurements were taken directly from soil samples taken with Guala 1664 (listed below): exchangeable Ca 0.1-0.3 Me/100g; exchangeable Mg 0.2 Me/100g; exchangeable Na 0.4-0.6 Me/100g; exchangeable K

0.02 Me/100g; total exchangeable bases (TEB) 0.4-0.6 Me/100g; cation exchange capacity (CEC) 1.5-2 Me/100g; base saturation 20-37%; CEC/100g of Clay (E/C) 57.9-86; TEB/100g of clay (S/C) 17.1-18.6; exchangeable sodium percentage (ESP) 2-3.9%; exchangeable potassium percentage (EKP) 1-1.3%; fine sand 4-7%; medium sand 79-83%; coarse sand 11-13%; Silt 0%; Clay 3%; hue of soil wet 10YR, dry 10YR; color value of soil wet 2.5, dry 5-6; chroma of soil wet 1, dry 1; bulk density 1.35-1.42 g/cm^3.

Additional specimens examined. ANGOLA. Bie, Moxico [sic]: Munhango, May 1937, Gossweiler 11243 (US); Munhango, May 1937, Gossweiler 11246 (US); Munhango, May 1937, Gossweiler 11323 (LISCJ, US).

ZAMBIA. Near Kaoma, 11 July 1994, Guala 1664 (FLAS, MRSC, PRE, US).

Figure 3-14. *Homozeugos katakton*. A. Portion of a phytomere showing ligule, and node. Bar equals 1 1m. B. Partial inflorescence. Bar equals 1 cm. C. Habit. Bar equals 10 cm. D. Transverse section of a portion of a leaf lamina. Bar equals 1 mm. E. Dissection of a spikelet: clockwise from bottom; three anthers, pistil, lodicule, palea, lodicule, fertile lemma, sterile lemma, second glume, first glume, callus. Bar equals 1 mm.

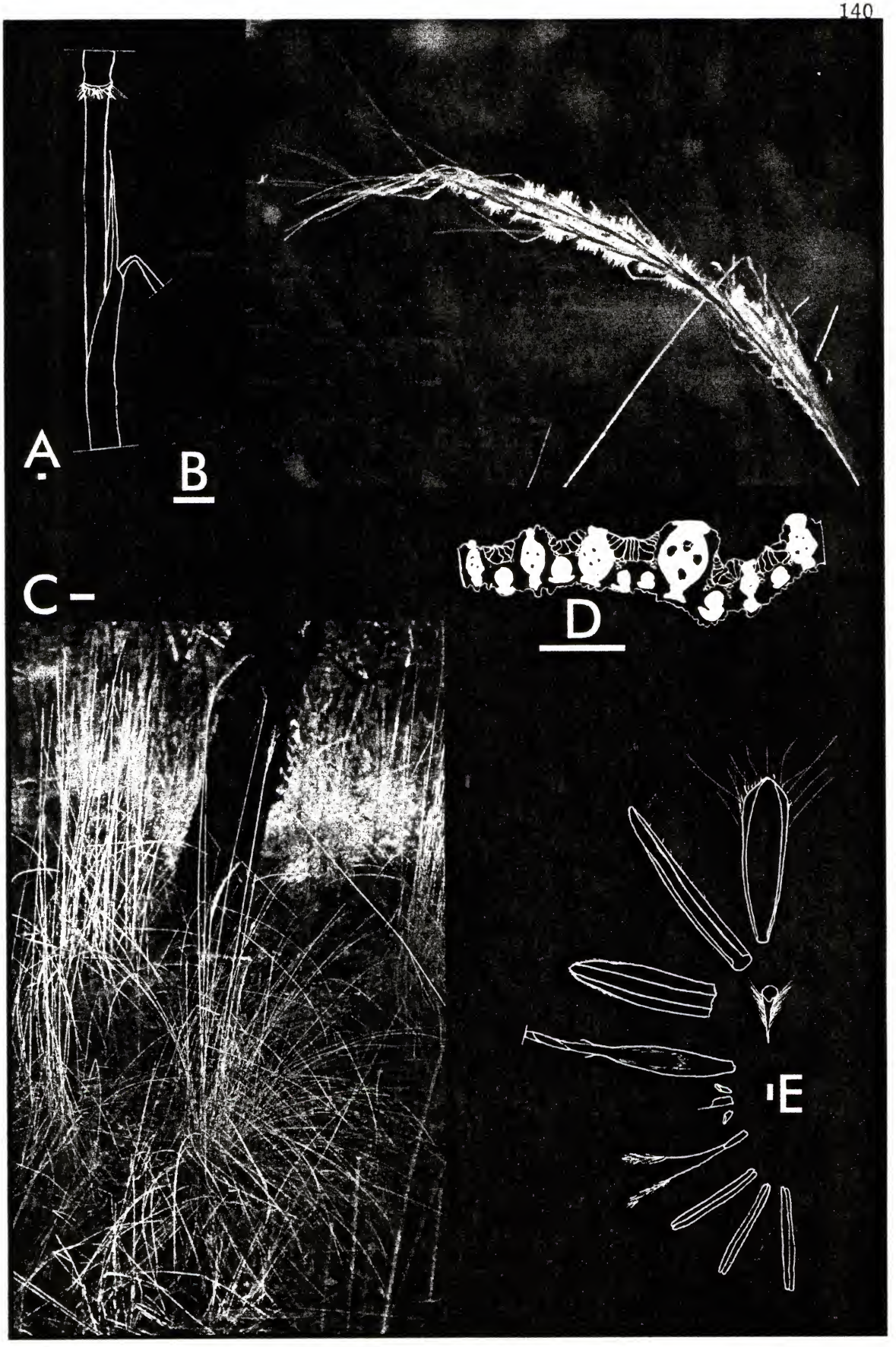
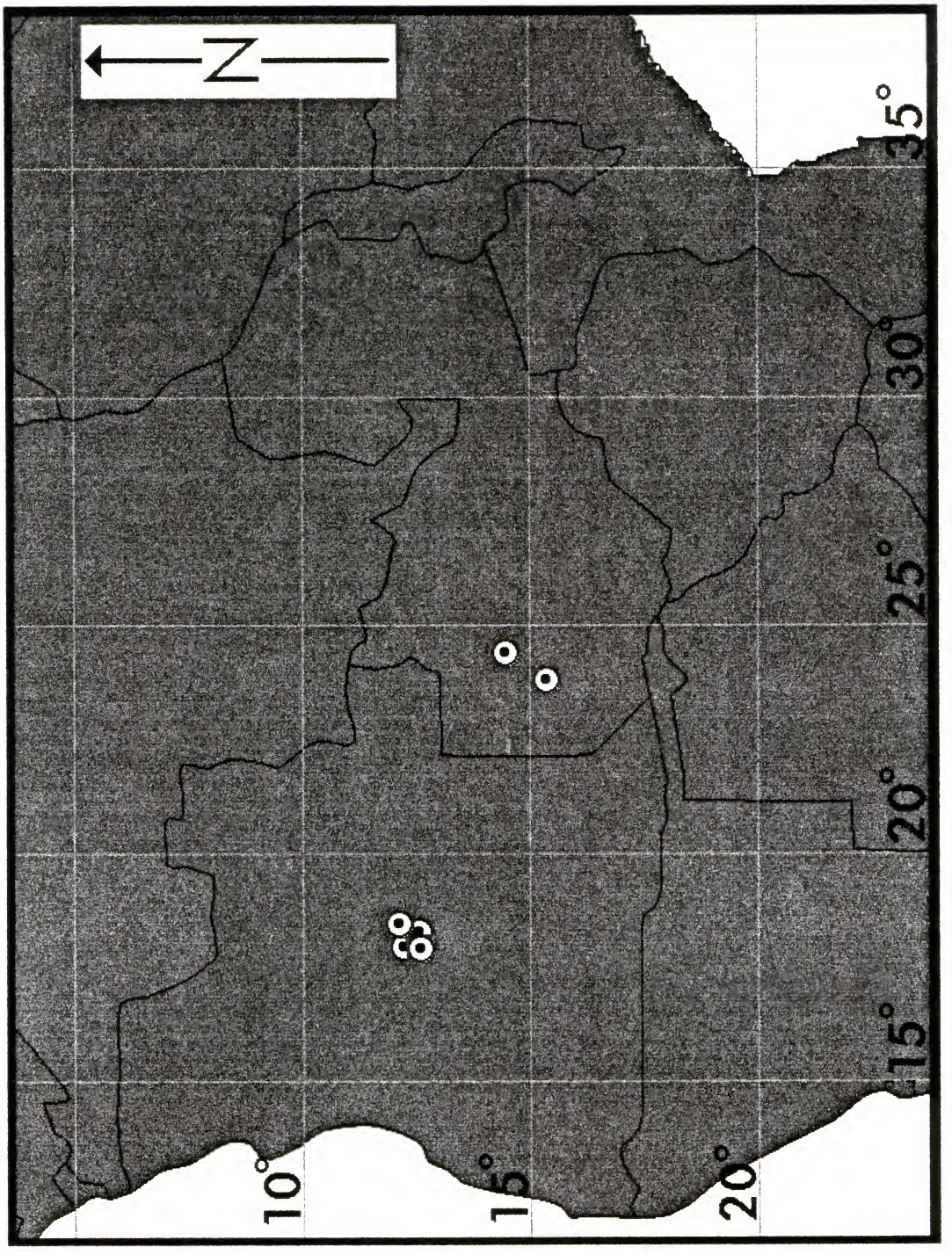

A
B
C
D
E

Figure 3-15. Distribution of *Homozeugos katakton*. Note: Verboom 1383 (mapped here at 14.63° S latitude and 24.53° W longitude) was reported by Clayton (1973) in the original publication of the species, but was not seen by me.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CHAPTER 4
SPATIAL HABITAT VARIABLES AND THEIR INTEGRATION WITH PHYLOGENY

Introduction

Each of the preceding two chapters has essentially been a self contained systematic monograph. They contain the cladograms, population distributions, and comparative data that are used here to generate maps of predicted potential distribution and make inferences about the relation of spatial distributions to phylogeny.

Two types of data are analyzed here. The most extensive data are a series of 45 layers of environmental parameters including temperature, precipitation and several physical parameters of the soil and habitat. Numerous studies have pointed to the importance of climatic factors in limiting the distribution of species (Cary *et al.* 1995, Dahl 1951, Nix 1975, 1986, Nix and Kalma 1972, Pigott 1954, 1974, 1975). Soil properties also have been shown to be important in delimiting the ranges of grass species at the mega-scale (Carey *et al.* 1995, Guala 1992, 1995) as well as the micro-scale (Bradshaw 1959, Jowett 1959, McNeilly 1968,

Shackleton and Shackleton 1994). Both scales are addressed in this study. The GIS includes soil variables at the mega-scale and the analyses of soil samples taken with each collection made for the study address micro-scale variation.

I employ a Geographic Information System (GIS) here to analyze the data. This is an integrated set of databases (a.k.a. coverages, layers, or themes). They are each like a spreadsheet with each cell in the spreadsheet representing a grid cell in a grid (in latitude/longitude in this case) of the area being examined (the whole earth in this case). Beyond the usual spreadsheet functions available within a layer, a GIS is also able to perform calculations vertically through multiple layers and output the result in the form of another data layer. This resulting layer can then easily be transformed into a map for graphical output. Most of the GIS data layers used here are derived through the use of worldwide point samples (weather stations, soil samples etc.) and an interplolating algorithm that uses values of other layers in conjunctions with a parameter specific algorithm to interpolate values for cells in the layer without directly sampled data. Other layers are derived more or less directly from satellite remote sensing data (often output in the form of satellite photos) with an interpretive algorithm used only to interpret the

relationship between the values in the satellite data and whatever parameter value (Generalized Vegetation Index, Albedo etc.) that they correspond to.

One must always be mindful that within a GIS there are an enormous number of sources of error, and that the reliability of these data may vary widely between layers and within them. See Figure 4-2 for an example. There is always the temptation to accept coverages as fact and to assume that alignments are perfect between layers. Neither of these should ever happen unless the layers are original and un-extrapolated data projected onto exact copies of the same base map. Of course, neither of these conditions can be met for areas larger than a few hectares or possibly a few square kilometers. A GIS is generally a primary visualization tool and a database of both measured and interpolated values. Fortunately, even the most rudimentary GIS is a very sophisticated visualization tool and database, which is ideally suited to working with spatial data.

The main goals of this chapter are to provide a paradigm for predicting the possible distribution of species, and for determining those spatial environmental parameters that have a correlation with cladogenic events. Such parameters are the most promising ones to examine for a direct relationship with the evolution of the group. They

also give us another parameter to consider when designing conservation strategies. The factors that are correlated with cladogenesis are those that will ultimately allow evolution to continue, thus allowing us to actually conserve species (not just preserve them) in the sense of Frankel and Soulé (1981). At least a large subset of these factors that are needed to affect true conservation must in some way be spatially distributed just as the organisms are. Thus a spatial database with a paradigm for predicting the significance of individual parameters is indispensable for true conservation.

Materials and Methods

Data layers. A geographic information system (GIS) was compiled from the data set, NOAA-EPA Global Ecosystems Database Project (1992), and converted to ArcView 3.0a (ESRI 1996, 1997) format. Although several other data sets were consulted and examined over the course of the study, only data from the NOAA-EPA CD-ROM were included in the final version of the GIS used for the analyses and maps presented here. The data sets were copied from the CD-ROM, converted from integer/binary format to real/binary format using the CONVERT module of IDRISI vers. 4.0 (Eastman 1992) and then converted to ArcView 3.0a format in order to exploit the

superior graphical capabilities of ArcView. The ArcView/ArcInfo format is also becoming the standard among biologists. Conversion of files from IDRISI to Arcview grid format was done manually on the layer of surface Albedo and the 13 surface temperature layers. All other layers were converted using an ArcView 3.0a Avenue script written and provided by Justin Moat of the Madagascar Biodiversity Project, Royal Botanic Gardens, Kew. Forty five data layers (or themes) were used in the GIS (Table 4-1) and each has inherent characteristics that may influence its accuracy and applicability. Surface temperature, precipitation and cloudiness data (each with 12 monthly means) are from the data set of Leemans and Cramer (1992) which was originally derived from Leemans and Cramer (1991). Although other precipitation and temperature data are available, these data were used for several reasons. First, they are complete and cover the entire study area. Second, they are all from the same source and were originally sampled on the same base map. Because of this, the numerous problems associated with re-sampling from different base maps and projections were avoided. Third, they appear to be more congruent, on a monthly basis, with my own field observations and comparisons with known data points than do other available data such as those of Legates and Willmott (1989, 1992).

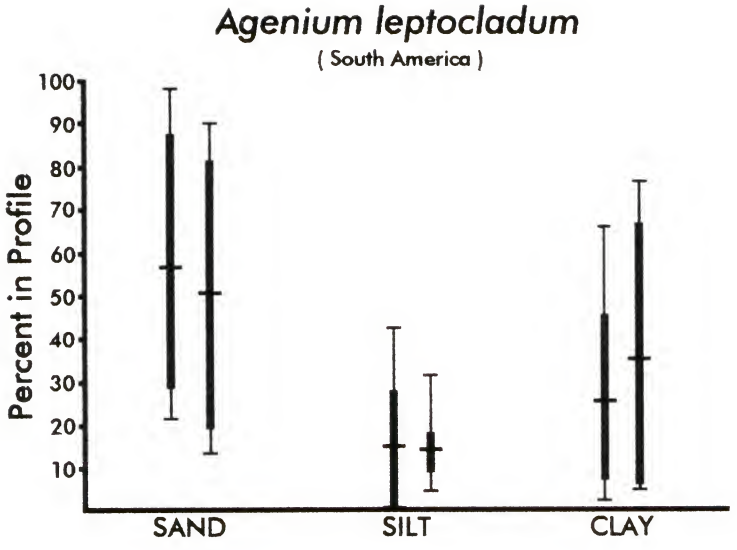
Table 4-1. Layers in the GIS.

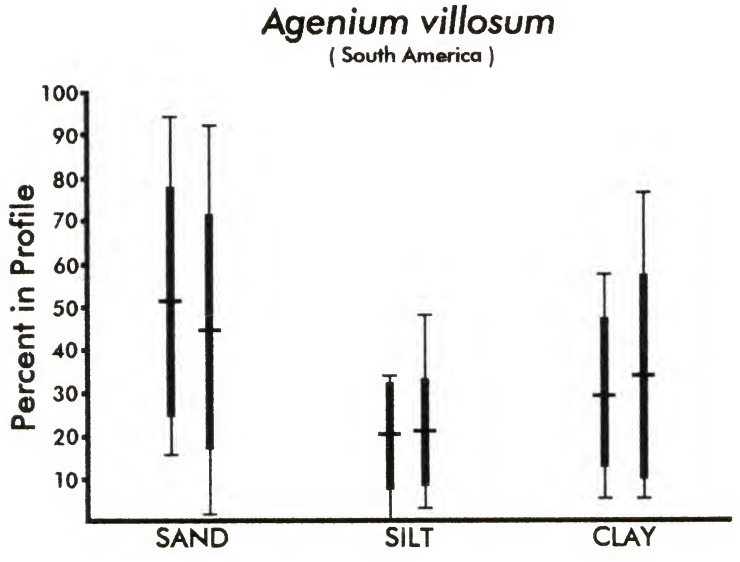
Layer Name	Reso-lution	Description
CloudJan - CloudDec (12 files)	1 Deg.	Percentage of actual bright sunshine hours as a percentage of potential sunshine hours per month.
TempJan - TempDec (12 files)	1 Deg.	Mean monthly temperature expressed as the number of 10ths of a degree Celsius.
RainJan - RainDec (12 files)	1 Deg.	Mean monthly precipitation expressed in millimeters.
Albedo	1 Deg.	Surface albedo in October expressed as percentage of possible X 100.
Elevation	5 Min.	Elevation in meters.
Rain	30 Min.	Mean annual precipitation expressed in millimeters.
Temperat	30 Min.	Mean annual surface temperature expressed in 10ths of a degree Celsius.
Sand	1 Deg.	Percentage of sand in the top 1 meter of soil.
Silt	1 Deg.	Percentage of silt in the top 1 meter of soil.
Clay	1 Deg.	Percentage of clay in the top 1 meter of soil.
GVIJan	10 Min.	Calibrated generalized vegetation index for January 1990.
GVIJul	10 Min.	Calibrated generalized vegetation index for July 1990.

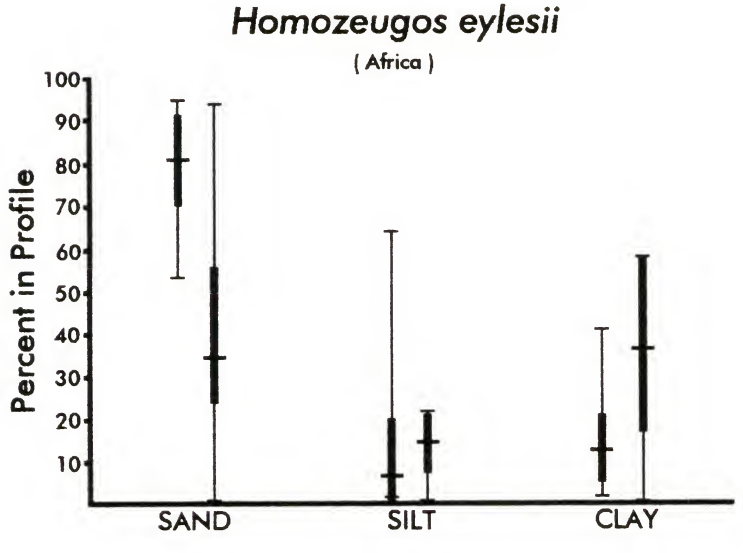
My own anecdotal comparisons were made using long term rainfall and temperature records from the Reserva Ecológica do IBGE in Brasilia, Brazil (years 1975-1994), rainfall from Rosslyn Safaris, Matetsi, Zimbabwe (years 1973-1995), and rainfall from the Matetsi Headquarters of the Zimababwe National Parks Service (years 1977-1992). The Leemans and Cramer data were closer to the long term measured monthly means in almost all instances. The Leemans and Cramer data are interpolated using a spatial model described in Leemans and Cramer (1992) from long term means for each month compiled from available station records from 1931-1960. The annual summaries of precipitation and surface temperature in the data set of Legates and Willmott (1989, 1992) were also used in the GIS because none were included in the Leemans and Cramer set. Although the Legates and Willmott set matched my anecdotal sets less closely on a monthly basis, the annual totals were within the range of known annual totals for each of my anecdotal sets and are probably more realistic given that they are calculated from actual annual means rather than the sum of monthly means that I would have employed if I had used the Leemans and Cramer data, which did not originally include annual means.

The other ten layers of the GIS were: elevation, surface albedo, the sand silt and clay content of the

Figure 4-1. Measured vs. predicted values for the percentages of sand, silt, and clay in the top 1 m of soil over the ranges of three species. Thin vertical lines represent the range, thick vertical lines represent one standard deviation around the mean, the thick horizontal line on each bar represents the mean. The bar on the left of each pair is from the actual measured percentages in soil samples collected in the top 15 cm of soil with each of my specimens and located using a GPS. The right bar of each pair is from the values extracted from the GIS for all collections (mine and borrowed herbarium material) that could be mapped from their label data. The data are ostensibly a prediction of the values in the top 1 m of soil but in practice, the data are most often taken from 15 cm samples as mine were.


Agenium leptocladum
(South America)
Percent in Profile
100
90
80
70
60
50
40
30
20
10
SAND
SILT
CLAY


Agenium villosum
(South America)
Percent in Profile
100
90
80
70
60
50
40
30
20
10
SAND
SILT
CLAY


Homozeugos eylesii
(Africa)
Percent in Profile
100
90
80
70
60
50
40
30
20
10
SAND
SILT
CLAY

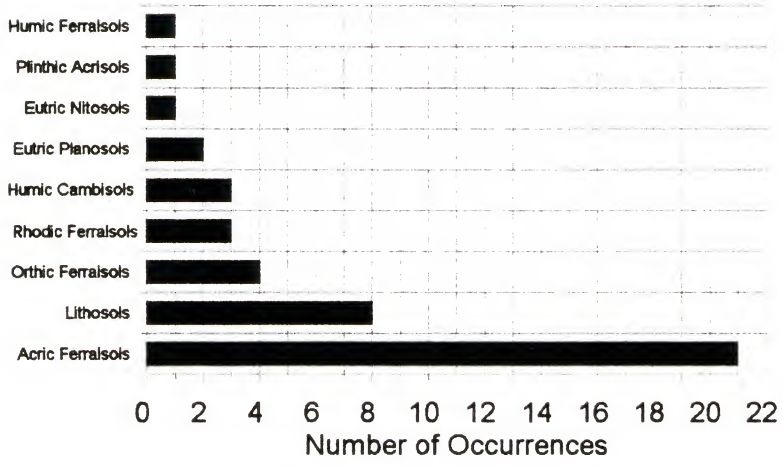
top 1 m of soil, and the generalized vegetation index GVI for January and July of 1990. Elevation data are from NOAA/NGDC (1992), a re-gridding of Edwards (1989). These data were the most accurate available for the regions in question when the project was begun. They are much more congruent with my own measurements in Florida, Africa, and South America than the Navy Terrain data (FNOC 1985, 1992) which are also widely available. The Edwards Elevation data (commonly known as ETOPO5) also are at a much finer resolution than the Navy data. This probably accounts for much of its increased accuracy in the rolling and rugged terrain that makes up much of my study area. The sand, silt and clay values in the top 1 m of soil are from Webb et al. (1991a, 1992). The values were calculated from an interpretation of the FAO Soil Map of the World (FAO-UNESCO 1981) and the World Soil File (Zobler 1986) using the algorithms described in Webb et al. (1991b). I have actual measurements for a large number of collections from three species and compared them to the predicted values in the GIS layers (Figure 4-1). The data show a close correlation in South America, but correlate less well for Africa. This is likely due to the very low data density in the remote areas of Zambia where *Homozeugos eylesii* is most often found. Preliminary studies showed albedo to be only moderately

definitive for species distributions so only one layer was selected for inclusion in the GIS. I used the October layer because it falls in the least variable period of the year for which data were available throughout most of the study area. The data are from Matthews (1983a, 1992) and are derived from a combination of cultivation intensity and vegetation as well as published sources and extensive satellite imagery using the techniques described in Matthews (1983b, 1983c). Global Vegetation Index (GVI) layers for June and July of 1990 were included because they present a relatively high resolution assessment of the vegetation density and greenness over the study area. January and July were chosen because they are always part of the wet and dry seasons respectively. Values from 1990 were chosen because they most closely match the mean in the study area for the years available (1985-1990). The "monthly experimental calibrated GVI" data layers were used from the data set of EDC-NESDIS (1992). They were developed from Gallo (1992) using methods described in Kineman and Ohrenschall (1992). The FAO/UNESCO soil units map (UNEP/GRID 1992), which is derived from the FAO Soil Map of the World in Digital Form (UNEP/GRID 1986), was also included in the GIS but was too big to manipulate with the other layers (230 MB in ArcView Format) and was subsequently removed. The soil types that

Figure 4-2. Occurrence of the species of *Agenium* on FAO soil types.

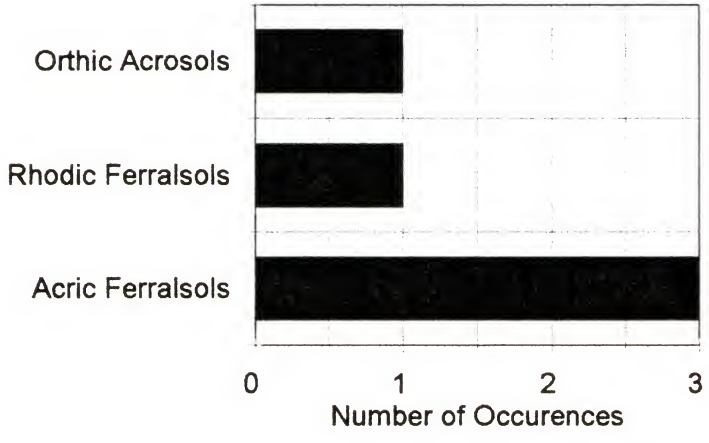
Agenium leptocladum

Occurrences on FAO Soil Types



Agenium majus

Occurences on FAO Soil Types



Agenium villosum

Occurrences on FAO Soil Types

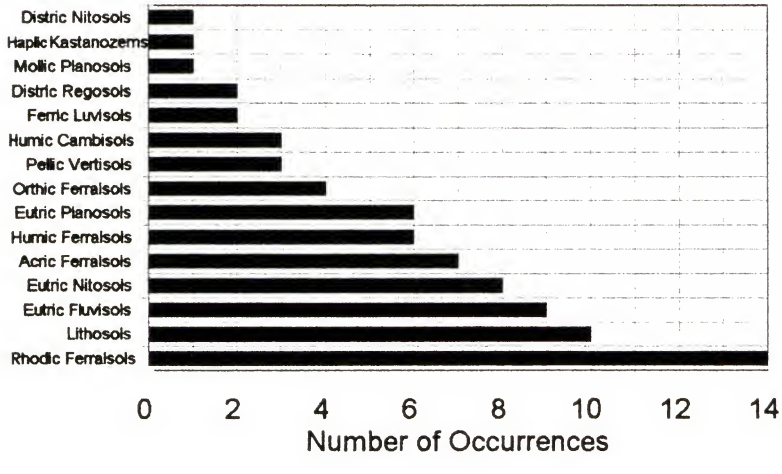
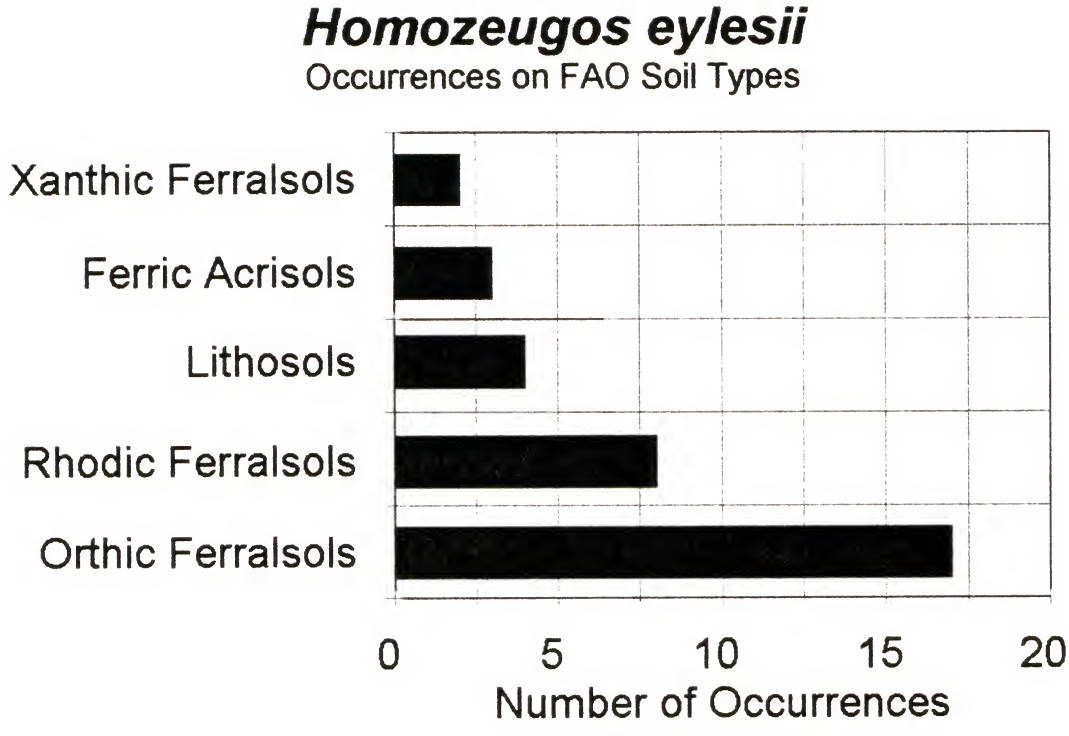


Figure 4-3. Occurrence of the species of *Homozeugos* on FAO soil types.



Homozeugos conciliatus - was collected from an area mapped as a Xanthic Ferralsol.

Homozeugos fragile and ***H. gossweileri*** - are likely to be from an area mapped as a Ferralic Arenosol.

Homozeugos huillense - was collected once in each of three areas mapped as an Orthic Ferralsol, a Xanthic Ferralsol, and a Lithosol.

Homozeugos katakton - was collected once in each of three areas mapped as a Eutric Gleysol, a Cambic Arenosol and a Ferralic Arenosol.

each species occurs on (according to the map) are given in Figures 4-2 and 4-3.

Each specimen examined for the monographs (Chapters 2 and 3) was mapped to a single point, which ranged from an informed guess in the case of weakly documented specimens to exact localities determined with a Trimble Ensign global positioning system (GPS) for all of my own collections. These were saved as degrees latitude and degrees longitude, to six decimal places in the various working databases and spreadsheets used in producing the monographs. Distributions of each species were saved from the spreadsheet as a Dbase file with three fields (latitude, longitude and a value field which contained the collection number). There were no identical collection numbers in the study set. These Dbase files were then imported into ArcView as tables and added to the View as an ArcView "event theme". Thus data could be retrieved and compared for each collection based on the collection number.

Each file was also subsequently converted (as a copy) to both a shape file and a grid to facilitate some manipulations and output within the GIS. A copy of each table was also made with the collection number in the value field replaced by "1", forming a single attribute data file for making species comparisons.

Figure 4-4. The range of values for mean monthly sunshine hours (CloudJan - CloudDec = A - L) taken from the known distribution of *Agenium leptocladum* and mapped over the world.

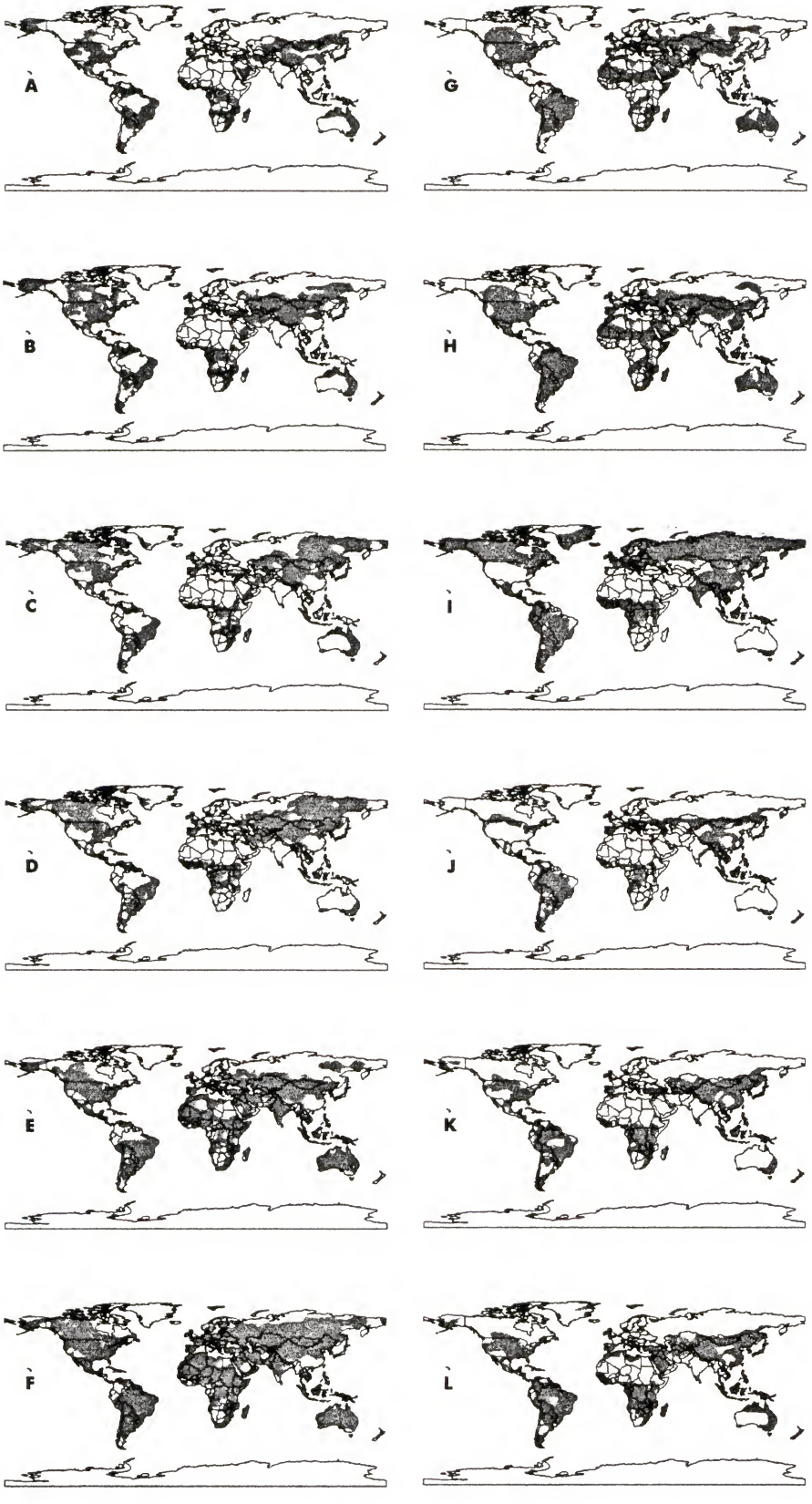

A
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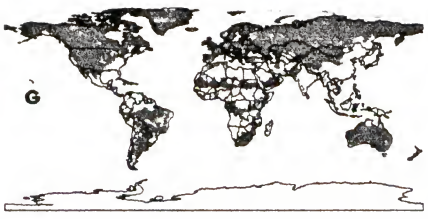
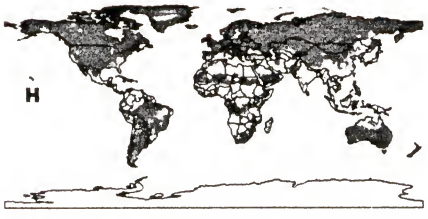
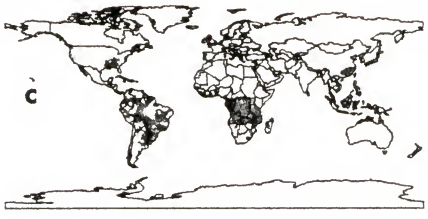
Figure 4-5. The range of values for mean monthly precipitation (RainJan - RainDec = A - L) taken from the known distribution of *Agenium leptocladum* and mapped over the world.

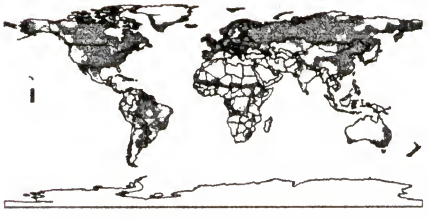
A


G

B


H


C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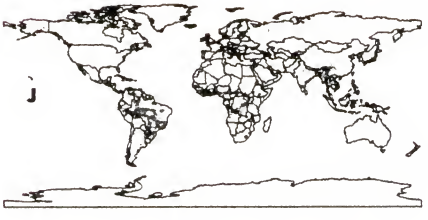
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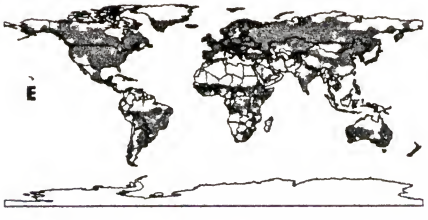
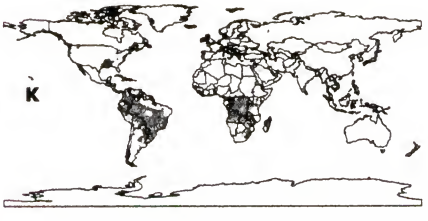
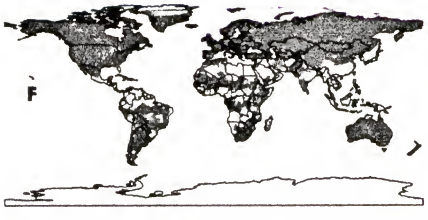

E


K


F

L

Figure 4-6. The range of values for mean monthly temperature (TempJan - TempDec = A - L) taken from the known distribution of *Agenium leptocladum* and mapped over the world.

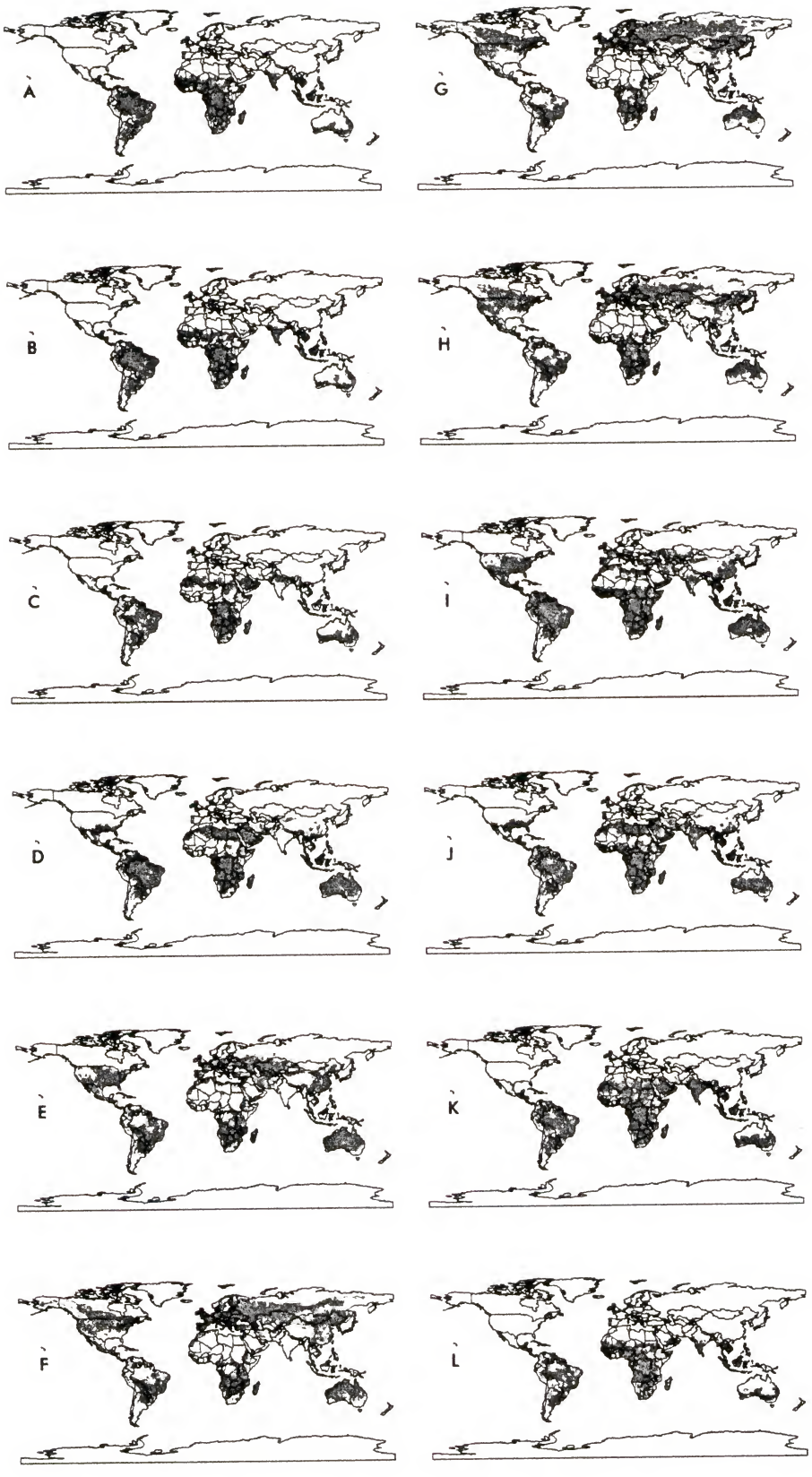

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Figure 4-7. A. Sand, B. Silt, C. Clay, D. Rooth2o, E. Soilh2o, F. Soiltxh2o, G. Albedo, H. GVIJan, I. GVIJul, J. Rain, K. Temperat, L. Elevation. All layers taken from the known distribution of *Agenium leptocladum* and mapped over the world.

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Predicted Potential Distribution Methods

To produce a predicted potential distribution of each species, the value of each of the 45 layers in the GIS was summarized for the points in each species distribution table. Maximum, minimum, range, mean and standard deviation were transcribed to a spreadsheet for later use. Each layer was then reclassified so that all cells with values falling between the previously determined maximum and minimum for the species in question were given a value of "1" and all other cells were given a value of "0". The set of reclassified layers for *Agenium leptocladum* is given in Figures 4-4 through 4-7.

All of the layers were then added together. Thus, a cell with a value of 1 in all of the reclassified layers would have a value of 45 in the sum of the maps. Each cell was then multiplied by 100 and divided by the total possible sum to give a percentage of the layers intersecting within each cell. The maps for each species are given in Figures 4-8 through 4-15.

Evolutionarily Significant Characters

A method for determining and comparing the different levels of evolutionary significance in the distributions of spatial parameters among species was developed in 1993

(Guala in press). The existing GIS and a database of physical and chemical analyses of soil samples that were taken along with every specimen collected for this study, were used for this analysis. All soil samples from South America were analyzed at the Centro de Pesquisa Agropecuária dos Cerrados (CPAC-EMBRAPA) in Brasilia, Brazil. The methods for both the chemical and physical analyses follow Empresa Brasilera de Pesquisa Agropecuária (1979). All soil samples from Africa were analyzed at the Soil Laboratory, Box X505, Causeway, Harare, Zimbabwe using the methods described in Millián (1988). Color value, hue, and chroma were determined by the author on wet and dry samples in full sun using a Munsell Soil Color Chart with the Tropical Soils Supplement. Bulk density was determined using a 100ml 3:5 aspect aluminum tube sampler and an Ohaus portable balance.

The primary method for comparing the ranges of spatial parameters to the cladogram is as follows.

1.) The GIS was queried for the values at each point of occurrence for each species (giving a range). This was done for all of the spatial environmental layers in the GIS (see Table 4-1 and Figures 4-4, 4-5, 4-6, and 4-7).

2.) The component (the number of nodes) of the cladogram topology for all species (Nelson and Platnick 1981, Michevich and Platnick 1989) was calculated. This is the

maximum possible component value.

4.) The ranges of GIS layer values were then mapped onto the cladogram as any character distribution would be. Ranges are additive down the tree. Note that values at the nodes are not character states of the hypothetical ancestor, only a sum of the clade. The value of either of the two terminal taxa would be equally parsimonious assumptions for a hypothetical ancestor, thus the sum is simply the least likely to produce discontinuities between clades and is thus the most conservative estimate.

5.) Nodes that showed a discontinuity in their values between sister groups were labeled as informative and counted (this is the component value with respect to cladogenic events in this cladogram, of the environmental parameter contained in the GIS).

6.) This component value for a single parameter mapped onto the cladogram was then divided by the total possible component value (i.e. if there had been a discontinuity at every node) to produce an index value. A cladogram with a spatial parameter mapped onto it is presented in Figure 4-16.

Note that the method, as originally described by Guala (in press), incorporated measurements of both the component and the term of each spatial parameter on the tree.

Figure 4-8. Predicted potential distribution map for *Agenium leptocladum* in South America.

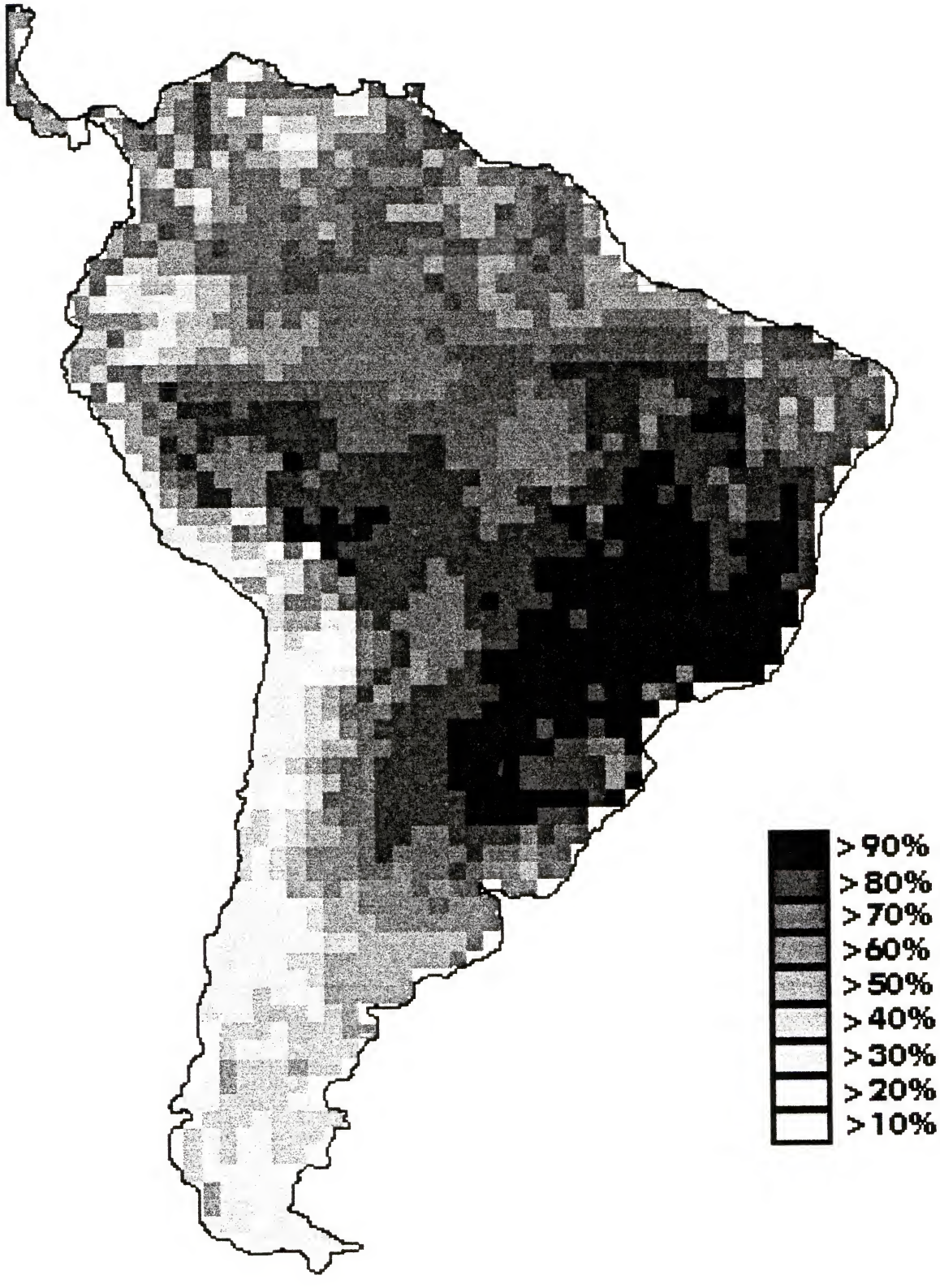
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Figure 4-9. Predicted potential distribution map for *Agenium majus* in South America.

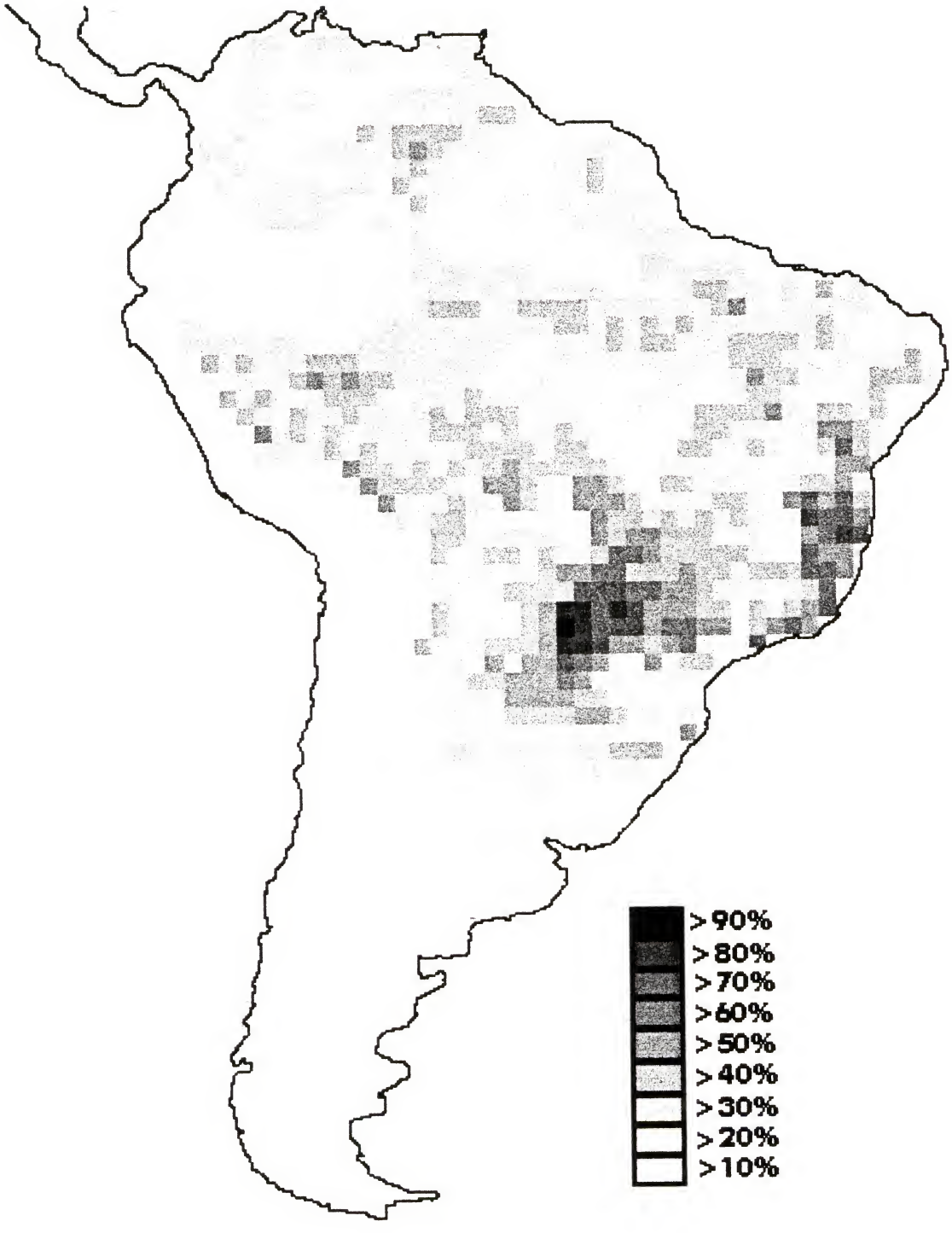
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Figure 4-10. Predicted potential distribution map for *Agenium villosum* in South America.

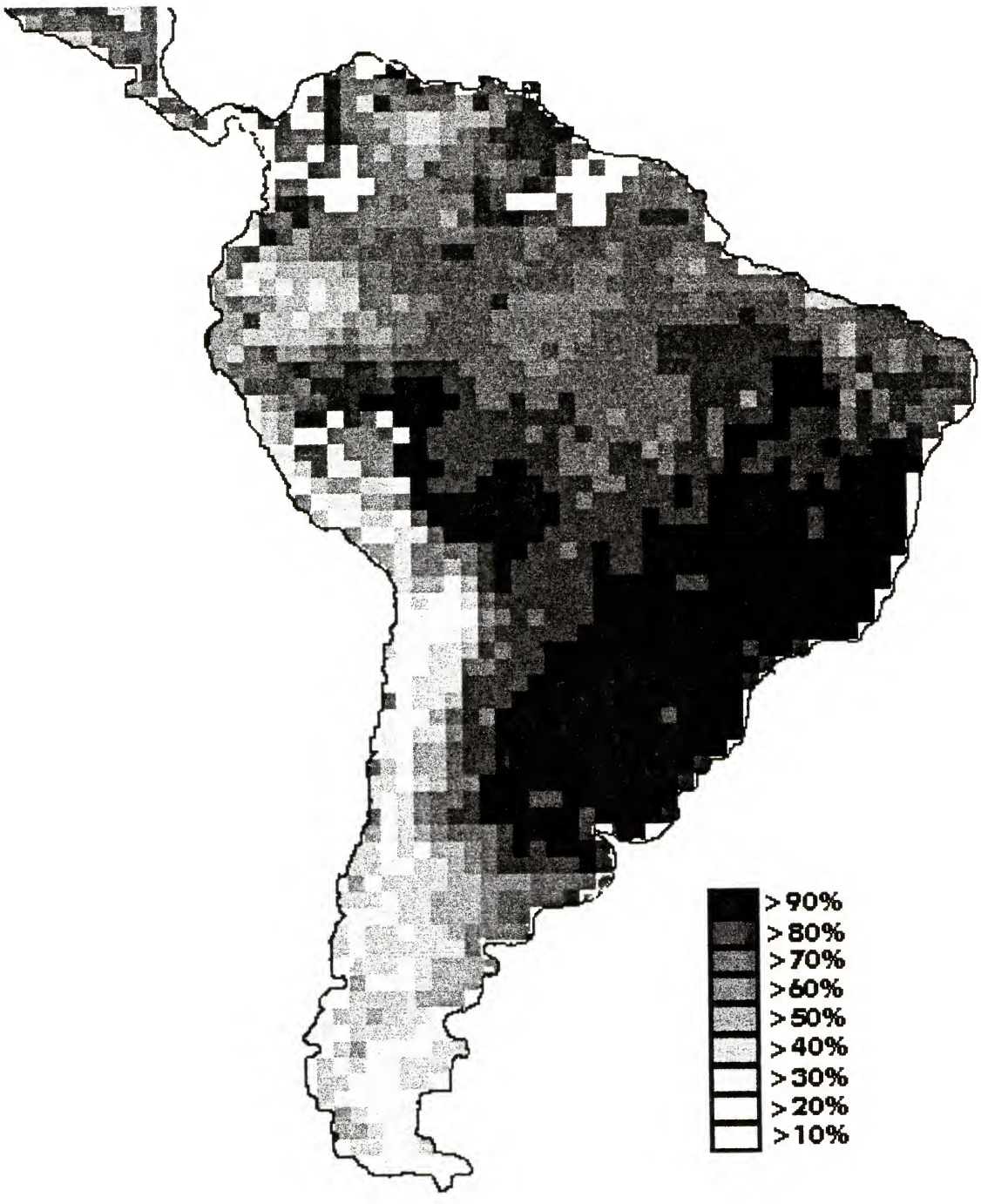
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Figure 4-11. Predicted potential distribution map for *Homozeugos conciliatus* in southern and central Africa. Less than ten percent of the layers overlap at any point on earth outside of the shown area.

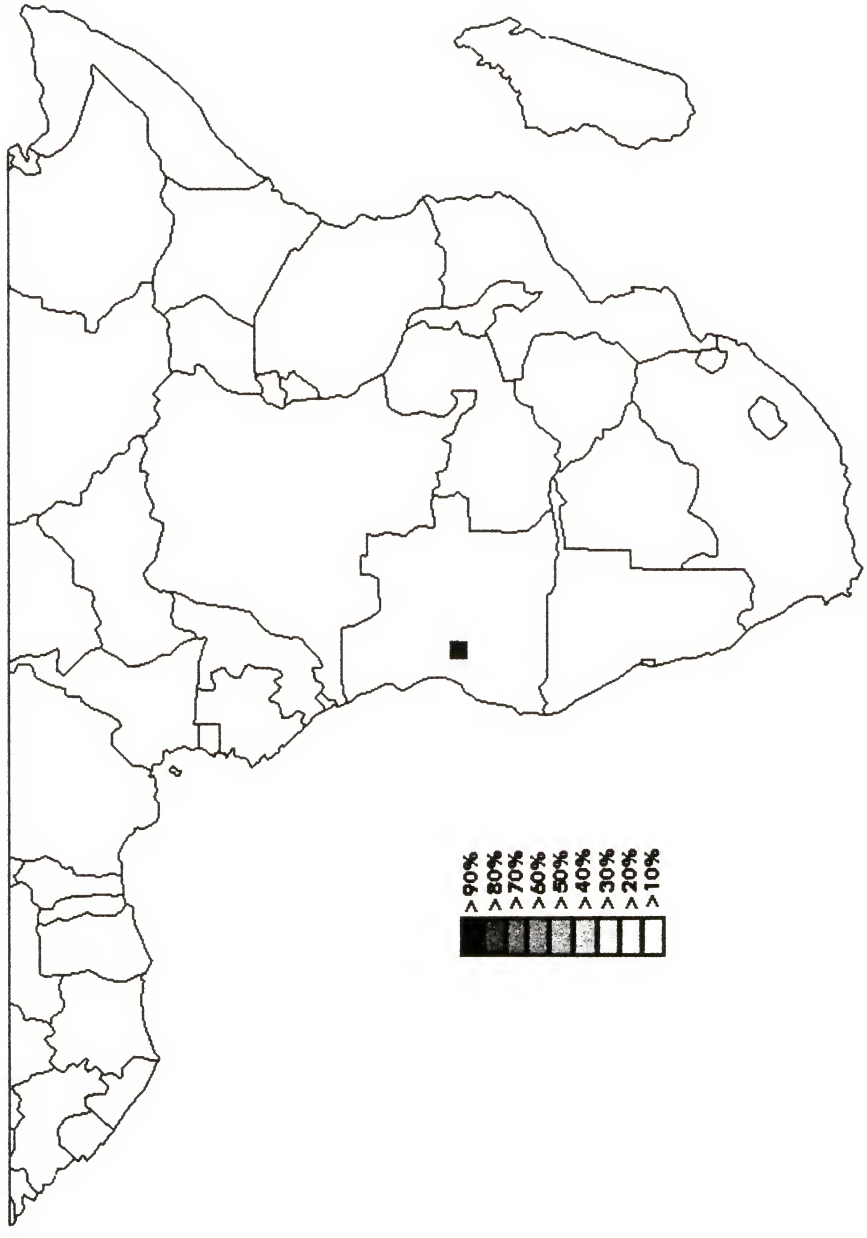
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Figure 4-12. Predicted potential distribution map for *Homozeugos eylesii* in Africa.

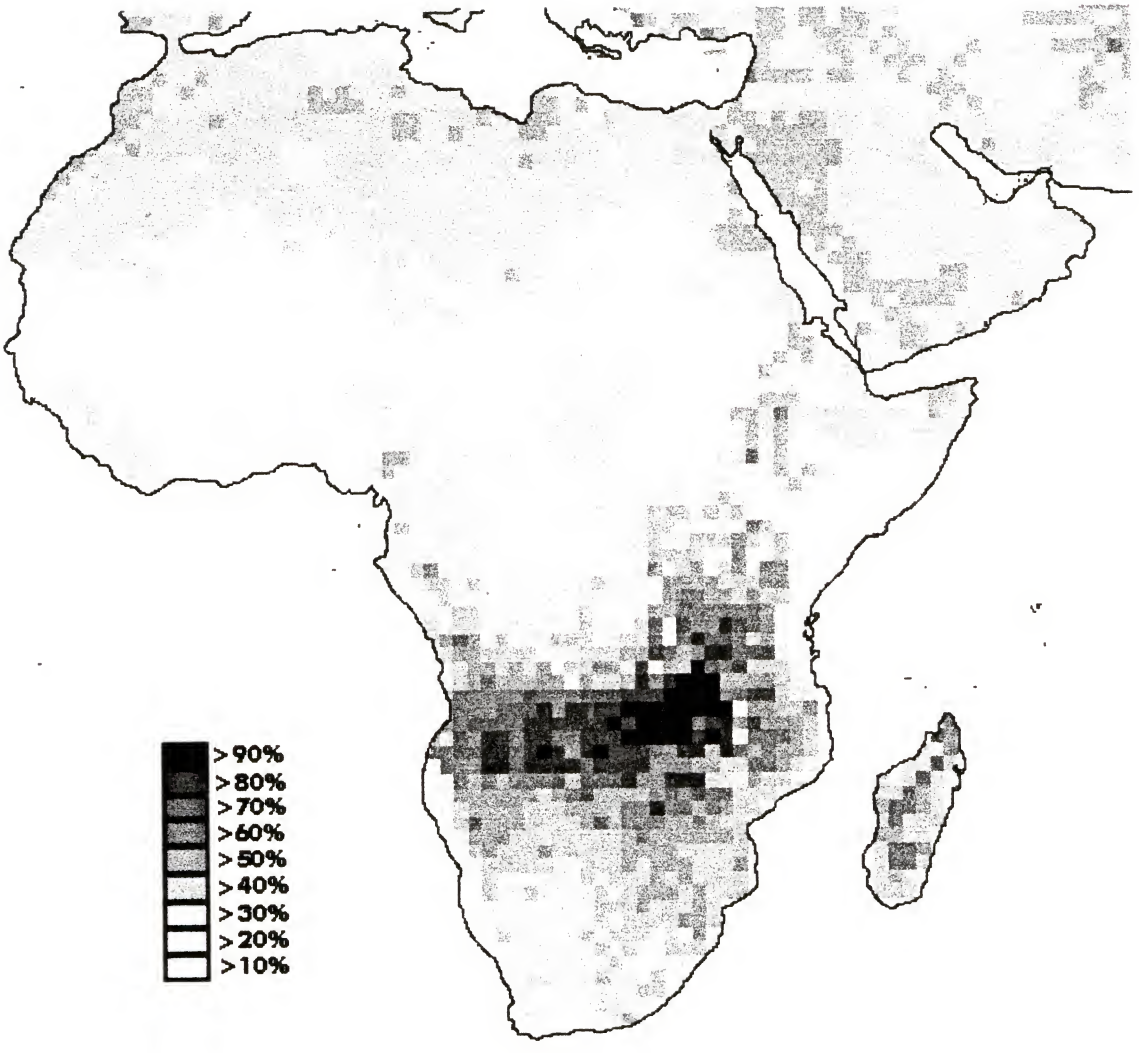
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Figure 4-13. Predicted potential distribution map for *Homozeugos fragile* and *Homozeugos gossweilerii* in southern Africa. Note: these species are each represented by a single collection. Both specimens were collected in the same area and could not be spatially differentiated from each other based on the label data. There is less than 10 percent overlap of layers outside of the area shown.

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Figure 4-14. Predicted potential distribution map for *Homozeugos huillense* in Africa.

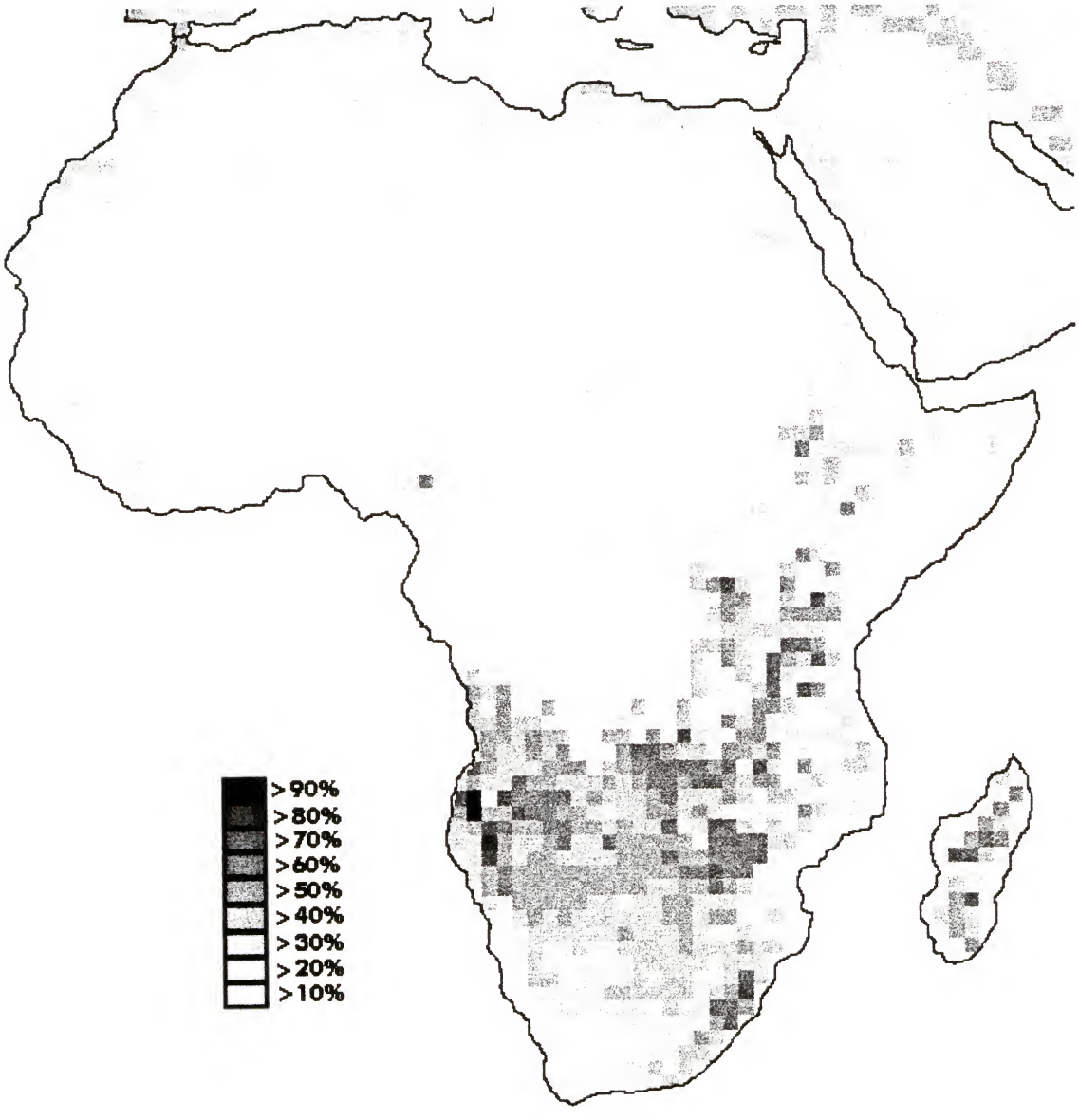
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Figure 4-15. Predicted potential distribution map for *Homozeugos katakton* in Africa.

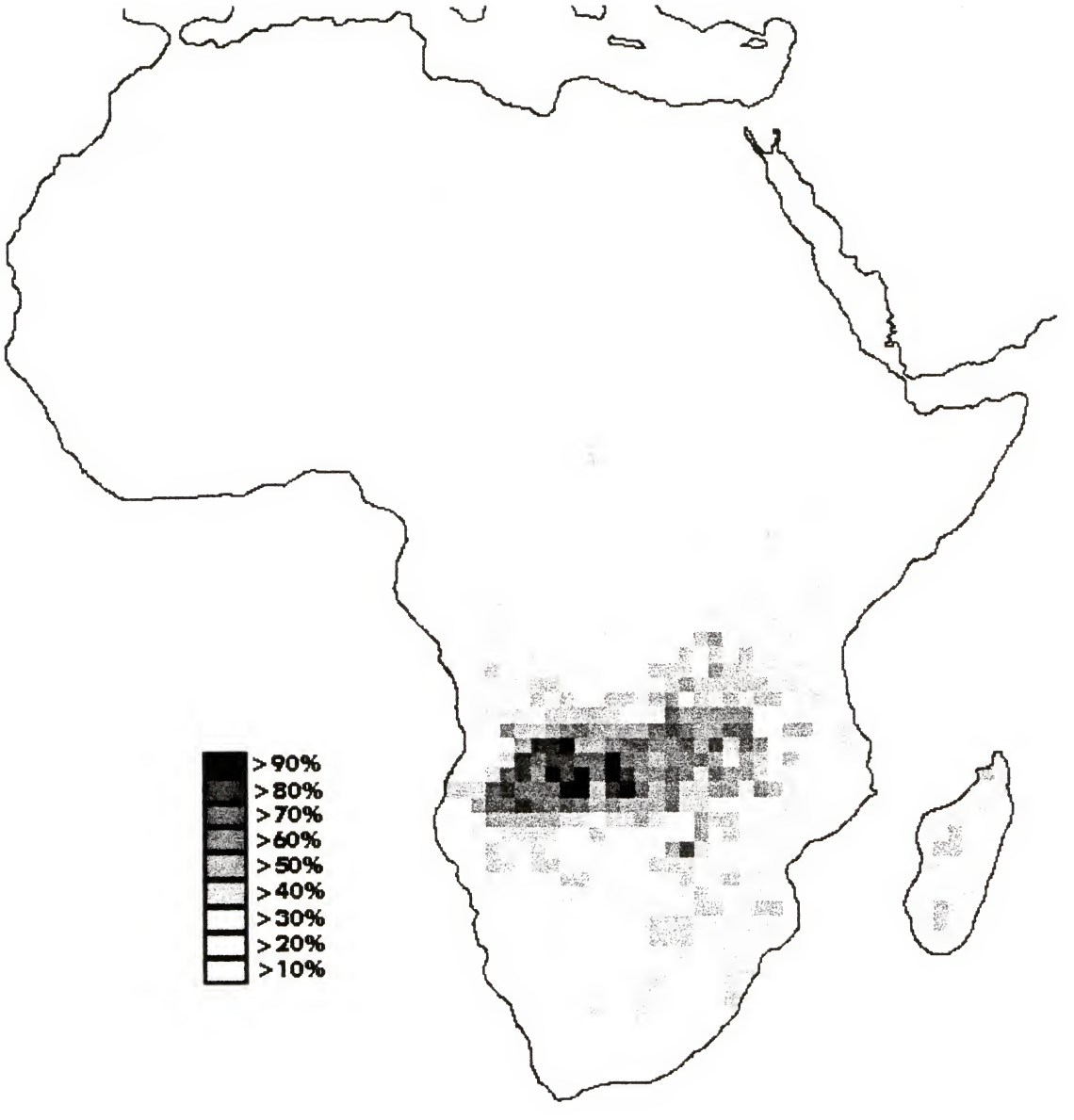
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Figure 4-16. A sample environmental parameter range (CloudOct) mapped onto the cladogram of *Homozeugos*.

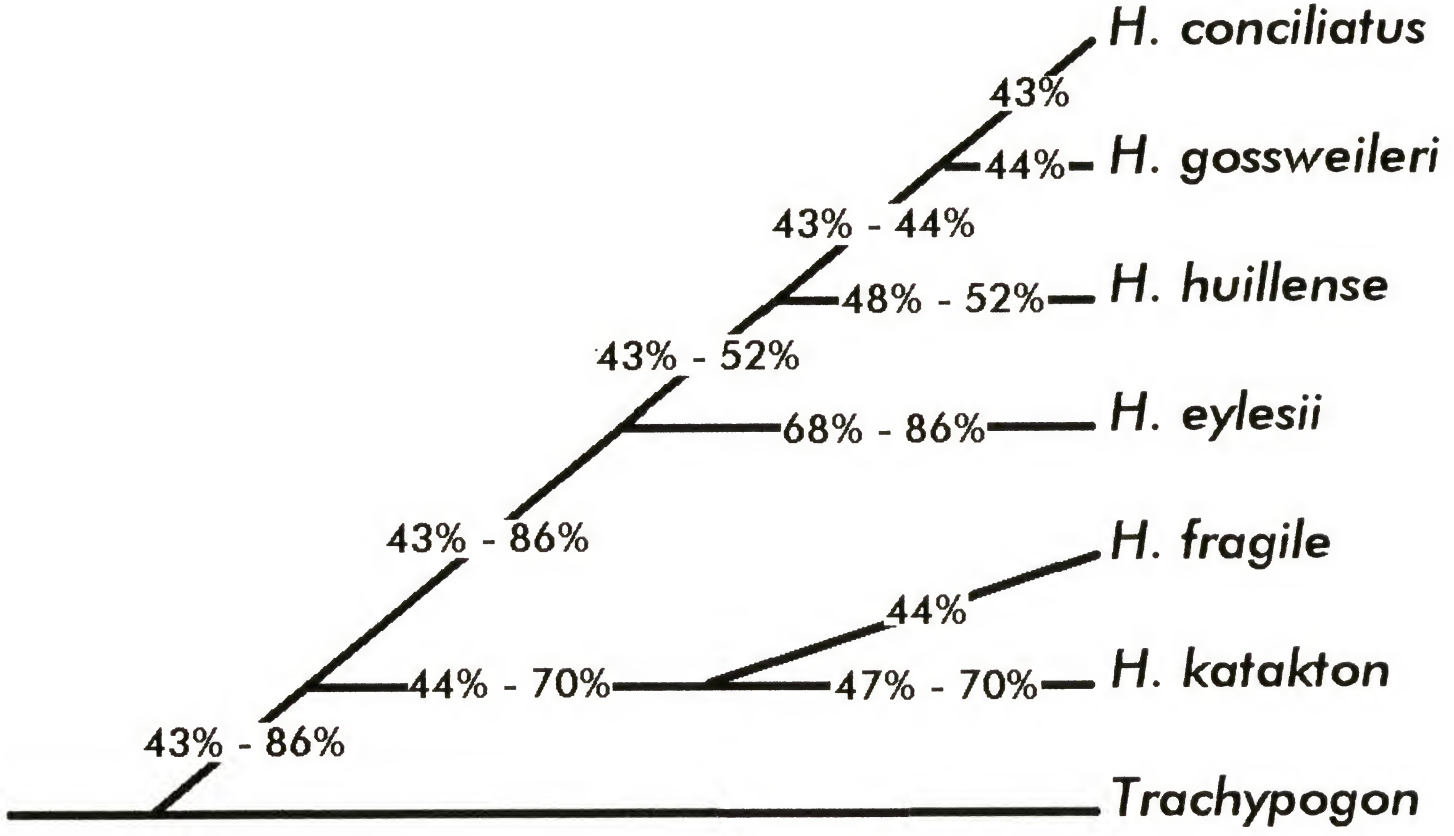
H. conciliatus
43%
44%
H. gossweileri
43% - 44%
48% - 52%
H. huillense
43% - 52%
68% - 86%
H. eylesii
43% - 86%
H. fragile
44%
44% - 70%
47% - 70%
H. katakton
43% - 86%
Trachypogon

Table 4-2. The component and index values of the spatial environmental parameters in the GIS that showed discontinuous variation among the species of *Homozeugos*. Values are computed from the cladogram for Homozeugos (Fig. 3-5). The total possible component score for the cladogram is 5.

GIS Layer	Component Score	Index Value
CloudApr	2	0.4
CloudAug	3	0.6
CloudFeb	1	0.2
CloudJan	1	0.2
CloudJul	2	0.4
CloudMay	2	0.4
CloudNov	2	0.4
CloudOct	4	0.8
CloudSep	3	0.6
Rain	2	0.4
RainApr	3	0.6
RainJan	3	0.6
RainNov	3	0.6
RainOct	3	0.6
RainSep	2	0.4
TempNov	2	0.4
Temperat	2	0.4
GVIJul	2	0.4

However, in a fully bifurcated tree, there is a two to one relationship between the term and component, so there is no need to record the term when the tree is fully resolved as in (Figs. 3-3 and 4-16).

The determination of which nodes were informative was influenced by the delimitation of character states. Although every method of dividing characters into states is laden with pitfalls (Stevens 1991, Stevens and Gift 1997) in this case a gap-based approach relying on discontinuities of one data unit or more seemed to be the most defensible. Because the data were, for the most part, originally continuous data extrapolated from the geographic positions of the total number of known populations, there should be no missing data that can be estimated or assumed. Furthermore, a large number of variables in a large number of different units were considered, making impossible any kind of standardization of units needed to justify a specific gap size larger than the resolution of the data set. What are really being examined here are correlations of environmental parameter distributions (at the mapped spatial resolution currently available) with cladogenic events that are "diagnosable" at the current level of resolution.

Results

Predicted Potential Distribution Maps

The predicted potential distribution maps for each species are given in Figures 4-8 through 4-15.

Evolutionary Significant Characters

There were no completely discontinuous spatial parameter distributions between the species of *Agenium* in the GIS. Among species of *Homozeugos*, there were 18 spatial parameters in the GIS that showed discontinuities. The component and index value of each of these parameters is given in Table 4-2.

Discussion

Predicted Potential Distribution Maps

The ranges of species are likely to have been studied for as long as species have been recognized but it wasn't until the 1950's that important work on the direct linkage of these ranges to specific spatial parameters began to emerge. Classic papers are Dahl (1951), which examined the

limitation of the range of alpine plants in Scandinavia, and early papers on the flora of Britain by Pigott (1954, 1974, 1975). The first work on potential spatial distributions to be done in a modern, integrated way with a rudimentary GIS using multiple spatial parameters was that of Nix (1975) and his students and coworkers (Nix and Kalma 1972, Nix *et al.* 1977) in Australia. This work evolved into the present state of the art in prediction of species ranges using elaborate GIS-based models, with programs such as BIOCLIM (Nix 1986, Busby 1991, McMahon 1996) and the GARP model currently under development at the Environmental Resources Information Network (ERIN) in Australia (see http://www.erin.gov.au/general/biodiv_model/ERIN/GARP/garp.html). BIOCLIM is a crop based program that relies on climate to predict where different types of plants will grow by using surrogate terms (bioclimatic parameters) derived from mean monthly climate estimates. When reliable digital elevation models (a necessary component for using BIOCLIM) become available for the study areas, I will explore its possibilities.

The model used here to predict distribution is very rudimentary but its simplicity makes it more flexible and widely applicable. Parameters can easily be included or excluded in order to assess their significance in the

distribution and any spatial parameter can be employed as a raw or weighted parameter.

In the analyses shown in Figures 4-8 through 4-15, all parameters are equally weighted. The percentage output allows standardization with differing numbers of layers. This is a useful index because some layers contribute little or nothing to the delimitation of the predicted distribution. The percentage output is not a probability, only a description of the data. For the percentage to be comparable to a probability, one would have to assume that the layers constitute a random sample of all possible layers in niche space and that all layers are of equal importance within that space. This is clearly not the case. In the current GIS there was a minor problem with the averaging of the higher resolution data sets that excluded one or more of them from the analysis from time to time. I re-sampled the higher resolution sets and reran the analyses in order to correct this problem. However, the degree of relation to reality for most of the data sets is highly scale dependent. For example, cloudiness inherently varies at a relatively course scale, but elevation is inherently a fine scale phenomenon in the study area. The loss of resolution in the elevation layer through re-sampling is accompanied by what I consider to be an unacceptable loss of relation to reality

in that layer. Therefore I have elected to present the maps (Figures 4-8 through 4-15) using the data at their original resolutions in the calculations, and have corrected discrepancies with re-sampled data only when necessary. Thus, there is a small degree of incomparability but generally a higher degree of reliability in the maps.

Evolutionary Significant Characters

The goal of this analysis is to determine spatial environmental parameters that are correlated with cladogenesis and hence, possibly associated with such events. Unfortunately, there were no discontinuous spatial variables among the species of *Agenium*. It is not entirely clear why this is the case. No two species of *Agenium* were ever found growing together during my field work, although *Agenium leptocladum* and *A. villosum* were sometimes found within a few kilometers of each other, and *A. villosum* is known from the same general region as *A. majus*. This means that all but the most fine scale spatial variables will overlap in values. In *Homozeugos*, even though *H. fragile* and *H. gossweilerii* are mapped at the same point and *H. eylesii* has been collected near *H. katakton*, there are twice as many species and hence five internal nodes in the cladogram rather than two, giving a much greater chance for

discontinuity to occur. One might also expect that the smaller number of collections for most of the species of *Homozeugos* also contributes to the number of apparent discontinuities in this genus. With respect to the raw number of discontinuities, however, the relative effect is probably negated by the ambiguity in locality for the Angolan collections of *Homozeugos*.

The chart of component values (Table 4-2) shows that the relative cloudiness and rainfall are clearly correlated with cladogenesis in *Homozeugos*. It is not clear whether it is the amount of sun or rain per month that is important because of the obvious correlation between cloudiness and rain. Rainfall is limiting to plant growth in much of southern Africa, so it is quite reasonable to think that it would also be a driving force in cladogenesis. Another important point to note about the analysis is that the only month for which temperature appears as significant is November, which is neither the warmest nor the coldest month of the year. It is, however, the beginning of the growing season and may be part of a complex interaction with precipitation. The appearance of GVI for July among the significant parameters is interesting because it is a measure of greenness in the driest month of the year, when all of the grasses are brown. This may actually signal a

primary habitat shift between areas with differing levels of woody cover because some species of shrubs and trees, such as *Acacia albida* Delile, *Cassia abbreviata* Oliver, and *Colophospermum mopane* (Kirk ex Benth) Kirk ex J. Léonard, are green in the study region during the dry season.

The effect of the ambiguity in the recording of collection localities that forces the mapping of *Homozeugos fragile* and *H. gossweilerii* at the same point and their respective places in the cladogram, i.e., one in each of the two largest clades, should also be noted. Although there are five nodes in the cladogram of *Homozeugos*, the maximum possible component value in this data set is four, not five, because both *H. fragile* and *H. gossweilerii* will have the same value for any layer in the GIS. This means that there can be no discontinuity in their common node at the base of the cladogram.

A second independent set of spatial data was the soil analysis that was done on samples taken with all of the specimens collected for this study. The complete data from these are included in the habitat descriptions in the taxonomic treatments in chapters 2 and 3. In *Agenium* there were no discontinuities between the two species, i.e., *A. leptocladum* and *A. villosum*, for which samples were collected. In *Homozeugos*, only a single collection of *H.*

katakton was made, in contrast to the 27 collections of *H. eylesii.* There were discontinuous differences between the two species in the silt, fine sand, medium sand and total sand fractions of the soil. The sand fraction data extracted from the GIS are not discontinuous in this set but it is clear from Figure 4-1 that these data may not be entirely reliable in Africa. Conversely, there is only one collection (with three replicates from the same population) of *H. katakton* in the measured values and the ranges of values for each of the measured variables will almost certainly expand when more populations are sampled. Because there are data for only two of the six species in the genus it is not realistic to apply these data to the cladogram, but these preliminary results do emphasize the importance of both physical and chemical analyses of the soil in future work.

Although sampling of soils was incomplete, there are weak indications that the physical properties of the soil may correlate with cladogenesis in *Homozeugos*. In contrast to the weakness of the soil data, the GIS environmental layers provide a clear indication that precipitation (or the lack of it) and the associated layers describing the percentage of sunshine hours per month are parameters that are associated with cladogenic events. There is also an

indication that temperature, at least in the beginning of the growing season, may also be linked to cladogenic events. The GVI for July is also interesting in that it may signal a habitat shift during a speciation event.

Distributions with respect to environmental parameters have other uses as well. For example, in chapter 4 *Homozeugos huillense* was found to be a metaspecies. The spatial data examined here from an independent data set, provide support, albeit weak, for the recognition of the taxon as a species. *Homozeugos huillense* has a unique range of values in the GIS layers: CloudAug, CloudDec, CloudJan, CloudJul, CloudSep, Rain, RainJan and GVIJul. This means that it occupies a definably unique niche that is likely to require unique, although possibly very subtle, physiological adaptations. These adaptations can be taken as autapomorphies for the species.

In summary, the clear phylogenetic hypotheses and distributional data included in a modern systematic revision are the raw data that can be integrated with a GIS to precisely predict ranges, determine environmental parameters associated with cladogenesis (and ultimately biodiversity) and to supplement phylogenetic hypotheses.

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BIOGRAPHICAL SKETCH

Gerald Franklin Guala II was born in Uniontown, Pennsylvania in 1965 and spent his early years in the halcyon hamlet of Hopwood at the foot of the Appalachians. Days in the garden with his great aunt and grandmother cultivated his interest in botany at a very early age. As a teenager he moved with his family to the pinnacle of Mt. Summit where the French and Indian War began. The deep woods and rugged topography inspired a consuming interest in wild plants. In the dense fog of humid summer evenings and the magical winter ice palace that appeared when nocturnal snows fell lightly on iced oaks and hemlocks, he found the beauty of nature and an inspiration to travel to magical and mystical places to study it.

In 1983 he went to Michigan State University to study botany. On the country's biggest college campus, surrounded by acid bogs, feral fens, tallgrass prairies, and beech-maple forests, he found that the only way to study everything was to study systematics. After five years of midwestern winters, he felt the need to migrate to Florida, and began his graduate program at the University of Florida.

After an initiation into the deep tropics in Brazil he came back and wrote his M.S. thesis: "All About *Apoclada*". Unable to leave Gainesville, he stayed on at the University of Florida and doubled his ambition in genera and continents, taking on *Agenium* and *Homozeugos* this time. He spent a few months following the Carnival in South America and then set off to Africa for a couple of years of lions at the door and snakes in the grass. After adventures in the backwoods of Zambia and the requisite malarial malaise he returned to Florida to finish his Ph.D.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Walter S. Judd, Chair
Professor of Botany

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Elizabeth A. Kellogg
Assistant Professor of
Botany, Harvard University

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Dana G. Griffin III
Professor of Botany

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Hugh L. Popenoe
Director and Professor of
International Programs

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May, 1998

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